Chapter 2

The Significance of Cyperaceae as Weeds

Charles T. Bryson and Richard Carter

ABSTRACT Weedy Cyperaceae adversely affect natural plant communities and the health of humans and livestock and are major deterrents to agricultural and forest productivity. Most weeds are exogenous and have traits that give them biological and reproductive advantages over other plants. Weeds cost billions of dollars in agriculture, forestry, and urban areas and threaten diversity in natural communities worldwide. Of an estimated 8000 species of weeds worldwide, only about 200 species cause approximately 95% of the problems in production of food, feed, fiber, and livestock. About 25% of the world’s weeds are monocots. Of these, sedges are among the most troublesome and difficult to control. The most important cyperaceous weeds in terms of their adverse effect on agriculture include Cyperus rotundus L., C. esculentus L., C. difformis L., C. iria L., and the Fimbristylis miliacea (L.) Vahl/F. dichotoma (L.) Vahl complex, ranking first, 16th, 32nd, 33rd, and 40th among the world’s worst weeds, respectively. We provide an overview of cyperaceous weeds, including economic losses, population dynamics, control methods, identification, biology, ecology, dispersal mechanisms, spread, and discussions of major weeds of agriculture, forestry, urban areas, and natural communities.

KEY WORDS Abildgaardia, Bolboschoenus, Bulbostyliis, Carex, Cladium, Courtoisina, Cyperaceae, Cyperus, Eleocharis, Fimbristylis, Fuirena, Isolepis, Kyllinga, Lepidosperma, Lepironia, Lipocarpha, Mapania, Oxycaryum, Rhynchospora, Schoenoplectus, Scirpodendron, Scirpus, Scleria, sedge, weed.
Cyperaceae is a cosmopolitan family with ca. 5000 species and 100 genera (Ball et al., 2002). Members of Cyperaceae, commonly called sedges, are monocot flowering plants with reduced, mostly wind-pollinated (anemophilous) flowers. The inconspicuous flowers are organized into spikelets, and the spikelets further arranged into higher order spicate, paniculate, or umbellate inflorescences. Flowers may be either perfect or imperfect, and when imperfect, plants are monoecious (or rarely dioecious). Fruits are small single-seeded achenes. Sedges are primarily grass-like herbs with linear leaves and parallel venation. Cyperaceae and Poaceae have traditionally been treated as related families (Cronquist, 1981). Recent cladistic analysis using molecular and morphological data confirms a closer relationship with Juncaceae, with the “sedge clade” consisting of Cyperaceae, Juncaceae, and Thurniaceae (Chase et al., 2000).

Many species of Cyperaceae are heliophytes, adapted to open, sunny areas with reduced competition from taller shading trees and shrubs. Such habitats are often dependent upon natural or artificial disturbance. A variety of plants, including many sedges, have intrinsic characteristics (e.g., high reproductive output, rapid growth, vegetative proliferation, extended seed dormancy) that promote population expansion after disturbance and probably originally evolved as colonizers of disturbed habitats (Baker, 1965, 1974; McNaughton & Wolf, 1973). In addition to catastrophic disturbances, more subtle and continual natural processes provide open areas for colonization by such species, e.g., exposed bars and banks along streams and coasts (Baker, 1974).

Plants are often called weeds when they opportunistically colonize and occupy habitats artificially disrupted and maintained by humans, e.g., agricultural fields, lawns, and gardens (Baker, 1974). The term “weed” is inherently anthropocentric and, therefore, is fundamentally problematic when used in science. Some definitions are entirely subjective and consequently are of little use in science, e.g., “a plant growing out of place” (James et al., 1991: 1) or “a plant growing where it is not desired” (Buchholtz, 1967: 389), and others emphasize only the negative effects of weeds on natural communities and ecosystems (Zimdahl, 1995; Randall, 1997). Although the latter are applicable to natural resource management and basic ecology, they are too restrictive for broader application to agriculture and other applied sciences. Bryson (2003: 1571) defined a weed as “an undesirable plant that adversely affects humans or other organisms which humans deem desirable.” Reducing further the anthropocentric emphasis and incorporating elements applicable in both pure and applied sciences, we propose the following definition: Weeds are plants that alter the structure of natural communities, interfere with the function of ecosystems, or have negative effects on humans, agriculture, or other societal interests.

Cronk and Fuller (1995) clearly distinguish between invasive plants that invade natural areas and weeds or ruderals that infest agricultural or other highly disturbed, artificial habitats, and they provide a system of ranking weeds and invasive plants. The same characteristics that enable plants to colonize an area during ecological succession can make them invasive pests when they are introduced outside their natural ranges or habitats. Invasive weeds alter wildlife habitat by reducing quantity and quality of food sources, nesting sites, and cover, by increasing the frequency of fire and soil erosion, and by changing the natural dynamics of aquatic systems causing flooding or desiccation. Contrastingly, in agriculture the most important weeds are those that have the greatest economic impact through reduction in crop yield, interference, or reduced efficiency or quality of harvest.

About 8000 species, or approximately 3% of the total number of plant species worldwide, have been documented as weeds (Holm et al., 1977). Of these, about 200 species, less than 0.1% of the world’s flora, account for approximately 95% of weed problems in agriculture (Holm et al., 1977, 1979, 1997). Invasive weeds possess a variety of characteristics enabling them to disperse rapidly into new areas and outcompete crops or native or desirable non-native vegetation for light, water, nutrients, and space (Westbrooks, 1998). To varying degrees, many characteristics contribute to the success and competitive-ness of invasive weeds, and sedges share many of these traits with other plants (Table 1). The number of weeds reported in crops and nonagricultural areas is increasing. Two decades ago the important weeds in cotton (Gossypium spp.) worldwide slightly exceeded 100 species (Holm et al., 1977; Cronk & Fuller, 1995). Because of changes in production and cultural practices (especially reduced-tillage production
systems), chemical control methods, weed shifts, adaptations of populations, evolution of herbicide-resistant weeds, and use of transgenic herbicide-resistant crops, the total number of important weeds in worldwide cotton production may currently exceed 200 species, as demonstrated by the total number recorded in cotton alone within the U.S.A. (Bryson et al., 1999). Natural barriers and restricted migration routes have historically prevented many plants from dispersing over great distances. However, the current speed and ease of world transportation by humans and cargo have increased the rate and distance of dispersal of plants. Upon introduction, if a species becomes naturalized, it may remain near the point of introduction without becoming a pest. In the case of invasive weeds, the local population amplifies and disperses, expanding the range. Unfortunately, newly introduced weeds often are undetected until after their numbers and ranges increase greatly. The period of time between introduction and invasion is the “lag phase” (Radosivich & Holt, 1984), the duration of which depends on a number of factors, e.g., size of population, dynamics of reproduction, and detection. The lag phase may vary from a few to many years, and facilitation of a naturalized population must occur before it expands, which may be brought about by new pathways for dispersal, introduction of new pollinators or dispersal vectors, environmental change (e.g., disturbance), and local adaptation through natural selection (Cronk & Fuller, 1995). Heterosis resulting from hybridization with related species may also be a factor in facilitation (Carter, 1990; Daehler & Strong, 1997).


<table>
<thead>
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<th>Characteristics of weeds.</th>
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<tr>
<td>Copious production of small seeds</td>
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<td>Early maturation</td>
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<td>Extended seed dormancy and discontinuous germination</td>
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<td>Germination and survival in a wide range of environments</td>
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<td>Long life of propagules in soil or during dispersal</td>
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<td>Profuse vegetative reproduction and fragmentation</td>
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<td>Rapid growth</td>
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<td>Short juvenile period</td>
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<td>Self-compatible or if cross-pollinated then by wind or unspecialized floral visitors</td>
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<td>Survival and the ability to produce seed under adverse environmental conditions</td>
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<td>Seed size similar to associated crops or native plants</td>
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<td>Structural modifications (e.g., thorns, prickles, spines, urticating hairs) that cause injury and repel animals or herbivores</td>
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<td>Structural modifications facilitating dispersal</td>
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<td>High photosynthetic rate (C₄ photosynthesis)</td>
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<td>Increased water-use efficiency (C₄ photosynthesis)</td>
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<td>Production of toxic secondary compounds that deter herbivores</td>
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<td>Production of phytotoxins to prohibit or suppress growth of other plants (allelopathy)</td>
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<td>Ability to parasitize other plants</td>
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<td>Accumulation of large food reserves in roots, rhizomes, or other plant structures</td>
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<td>Alternate host for insect pests and pathogens of crops</td>
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<td>Resistance to pathogens</td>
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<td>Small inconspicuous flowers</td>
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<td>Short- and long-range dispersal mechanisms</td>
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<td>Tolerance of environmental and chemical extremes, including fire, herbicides, and soil disturbances</td>
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ECONOMICS

There is little doubt that weeds cause severe economic losses, but placing an exact value on their impact worldwide is difficult, especially in natural or nonagricultural areas. In the U.S.A., economic loss due to invasive species (plants, animals, and pathogens) was estimated to be more than $138 billion per year (Westbrooks, 2001). Economic losses result from interference or competition with crops and forests and the costs of pest-control chemicals, fuel, equipment, labor, cultural-control practices, and additional irrigation and fertilizer (Chandler et al., 1984; Chandler & Cooke, 1992). Additional costs to human and animal health (i.e., allergies and toxins) are more difficult to estimate, but weeds, including sedges, cause substantial indirect economic losses worldwide.

In the U.S.A., it is estimated that cotton yields are reduced 8.5% by Cyperus L. weeds (Byrd, 1995a), a loss of about $40.5 million annually. The two primary Cyperus weeds in cotton and other row crops are C. esculentus L. (yellow nut sedge) and C. rotundus L. (purple nutsedge). In Mississippi alone, 31.4% and 23.5% of cotton fields are infested with C. esculentus and C. rotundus, respectively; however, population levels of C. rotundus were greater (75.6 aerial shoots/m²) than those of C. esculentus (21.8 aerial shoots/m²) (Byrd, 1995b). It is more difficult to estimate economic impact on nonagricultural areas, especially natural and public-use areas where losses are measured as reduction in tourism and recreation. Placing monetary values on native flora and fauna and wildlife habitat displaced or degraded by invasive species or the loss of the aesthetic value of a natural area is subjective and problematic. Control of weeds for the preservation of biological diversity is labor intensive and expensive, requiring manual labor where chemical methods may jeopardize natural plant communities (Randall, 1996). Upon control or eradication of invasive weeds, additional expense is incurred to prevent recolonization and to reintroduce native or innocuous nonindigenous niche replacements.

The importance of an agricultural weed is not necessarily correlated with its abundance within a crop but may depend on herbicide- and cultural-control regimes, soil type, climatic conditions, number of viable propagules in the seedbank, or other factors (McWhorter & Bryson, 1992). Some weeds may be abundant and conspicuous in crops without interfering, e.g., winter annuals that germinate, emerge, flower, and set seeds early enough so growth and yield of summer crops are unaffected. High population levels of Isolepis carinata Hook. & Arn. ex Torr. often occur in reduced-tillage cotton and soybean (Glycine max (L.) Merr.) in the southeastern U.S.A. (Bryson & Hanks, 2001). Because I. carinata completes its life cycle and dies early in the growing season, it does not adversely affect crop growth and yield. In agriculture, weeds that are difficult to control, compete with crops for light, nutrients, water, and space (Radosevich & Holt, 1984), interfere with crop harvest efficiency, or reduce quality of seed and lint (McWhorter & Bryson, 1992; Bryson et al., 1999) are the most important. Holm et al. (1977, 1997) list the world’s most important agricultural weeds. Lists of weeds maintained by organizations include the Weed Science Society of America’s Composite List of Weeds (WSSA, 1989) and Bayer AG’s Important Crops of the World and Their Weeds (Bayer AG, 1992). Bayer AG (1992) is a more comprehensive worldwide list and includes more than 5000 scientific names of crops and weeds, while the WSSA lists about 2000 weeds found exclusively in the U.S.A. and Canada. Since the second edition of Bayer AG (1992), rights to the five-digit “Bayer codes” for weeds have been sold to the European Plant Protection Organization.

The economic, ethnobotanical, and horticultural importance of the family Cyperaceae is well documented (Simpson & Inglis, 2001). Many sedges are used as foods, food additives, drinks, fibers, animal poisons, and in the manufacturing of items including paper, perfumes, medicines, mats, boats, clothing, shoes, ropes, and roofing (Kükenthal, 1935–1936; Zeven & Zhukovsky, 1975; Darby et al., 1977; Allan, 1978; Burkill, 1985; Negbi, 1992; Stephens, 1994; Bryson et al., 1998; Simpson & Inglis, 2001). Tubers, rhizomes, seed, and foliage of sedges are important wildlife and domesticated animal feeds or forage (Hermann, 1970; Miller & Miller, 1999; Abad et al., 2000). Cyperaceae are also utilized for erosion control, revegetation after natural disturbances, and to amend and improve soil fertility (Tachholm & Drar, 1950; Hermann, 1970; Burkill, 1985; Fagotto, 1987; Simpson & Inglis, 2001). Traits that make sedge species useful for erosion control and soil stabilization also make them weeds.
CONTROL METHODS

Control methods for weedy sedges are diverse. Cultural methods of hand removal, hoeing, and draft plowing are still used in much of the world to control weeds including sedges (Shear, 1985). Mechanical tillage, flame cultivation, mowing, chemical treatments (herbicides and fumigants), cover crops (e.g., sweet potato [Ipomoea batatas (L.) Lam.]), and shading with a crop or black plastic have proven to be effective in controlling many sedge weeds of turf, pasture, and vegetable and row crops (Patterson, 1982; Glaze, 1987; Bryson & Keeley, 1992; Buchanan, 1992; Peterson & Harrison, 1995). As shown by Bryson et al. (2003a) with Cyperus entrerianus Boeckeler, mowing alone will not effectively control certain perennial sedge weeds, but it can prevent seed production if mowing intervals are shorter than the time required to set fertile achenes. Fumigants are usually applied on small areas to sterilize the soil for vegetable crop production. Herbicide treatments may vary depending on the susceptibility of target species, crop tolerance, and required timing of application (McWhorter & Bryson, 1992). With each herbicide developed, research is conducted to determine the efficacy on weeds and the selectivity on crops (Holt et al., 1962; Hauser, 1963a, b; Duble et al., 1968, 1970; Hamilton, 1971; Hardcastle & Wilkinson, 1971; Keeley & Thullen, 1971; Keeley et al., 1972; Wills, 1972; Sandstra et al., 1974; Sandstra & Nishimoto, 1977; Wills & McWhorter, 1988; Grichar et al., 1992; Richburg et al., 1993, 1994; Wilcut et al., 1994; Vencill et al., 1995; Bryson et al., 2003b).

Effective methods of herbicide application include pre-emergence broadcast and incorporated (with tillage) applications to control unwanted sedges that germinate from seed, rhizomes, and tubers. Acceptable post-emergence treatments are dependent on the herbicide selectivity. Nonselective herbicides are applied in areas where nontarget species are of little concern, while selective herbicides are applied to control target sedges without harming crops or other desirable plants. Application technologies have been developed to spray or wipe nonselective herbicides on target weeds with special equipment (e.g., directed sprayers, hooded sprayers, recirculating sprayers, foam applicators, shielded sprayers, chemigation, control droplet applicators, air-assist systems, pneumatic applicators, sensing devices, electrically charged sprayers, and rope-wick applicators) to reduce or eliminate damage to crops (Burr & Warren, 1971, 1972; Wiese, 1986; Bryson & Wills, 1991; Wills et al., 1991; Barrentine et al., 1992; Bryson et al., 1992b, 1994a; Bryson & Hanks, 1993; Bryson, 1994, 1997). Directed sprayers and hooded sprayers are widely used in the U.S.A. for controlling Cyperus rotundus, C. esculentus, C. iria L. (rice flatsedge), and other weeds in cotton and soybean. Additives such as soaps and lightweight paraffinic oils effectively enhance activity of some herbicides (McWhorter, 1982; Bryson et al., 1990; Jordan, 1996). The development of herbicide-resistant, transgenic crops allows application of herbicides such as glyphosate over-the-top without damaging crops (Shaner & Lyon, 1980), while effectively controlling weeds. However, selection for herbicide-resistant sedges is a potential problem with the persistent use of a single herbicide or herbicide family (Dowler et al., 1974). Resistance to bensulfuron in C. difformis L. (smallflower umbrella sedge) populations is well documented in rice production (Pappas-Fader et al., 1993, 1994; Hill et al., 1994), and herbicide resistance is also known in other species (LeBaron, 1991).

Various pesticides also kill herbivores, predators, or pathogens of weeds, thereby potentially rendering weeds more competitive. For example, when nematocides control nematodes harmful to rice (Oryza sativa L.), they also kill nematodes attacking weeds of rice (e.g., Echinochloa spp. and Cyperus haspan L.) (Hollis, 1972).

Although several potential biological control agents (insects and pathogens) have been evaluated for controlling Cyperus esculentus, C. rotundus, and other sedges, none has been effective in reducing sedge populations outside controlled experiments (Phatak et al., 1987). It is unlikely that any single biological agent will provide total control of nutsedges (Morales-Payan et al., 2005). High parasitism and predation by other insects and use of pesticides that kill biocontrol agents are major constraints preventing effective biological control of sedges using insects in row crops (Frick, 1978). Excessive development, production, and registration costs, short shelf life, and ineffective delivery systems are major obstacles to utilizing pathogens.
for biological control of weeds (Boyette, 2000; Duke & Boyette, 2001).

**Population Dynamics**

Weed species and population levels differ depending on land use, cropland preparation, forestation, and disturbance in natural areas. In agricultural systems, weed shifts occur primarily when management practices or environmental conditions change (McWhorter & Bryson, 1992; Murray et al., 1992). A single natural occurrence (e.g., tornado, hurricane, earthquake, fire, flood) or cultural- and chemical-control practices in farming operations may eliminate or reduce populations of one weed, while enhancing the survival, growth, and reproductive potential of another. As an example, farmers in the southeastern U.S.A. claimed that *Sida spinosa* L. seed and some sedge weeds such as *Cyperus esculentus* and *C. rotundus* arrived in containers of dinitroanaline (DNA) herbicides. In actuality however, DNA herbicides controlled annual grasses and small seed broadleaf weeds and vacated a niche for other weeds to invade areas previously not infested (Frans, 1969; Dowler et al., 1974). Weed shifts may also occur when environmental factors are modified through row spacing, irrigation, and crop rotation in row crops or when irrigation and fertilization frequency is increased on lawns, turf, and flowerbeds. In row crops, many sedge weeds thrive on irrigated soils and occur in higher population levels prior to crop canopy closure. Canopy closure earlier in the growing season shades weeds and prevents seed or tuber germination; thus, it is an effective cultural practice in controlling many weeds, including sedges such as *C. esculentus* and *C. rotundus* (Bryson et al., 1990, 2003b).

Weed shifts may also occur as weeds disperse into new areas. Non-native weeds, such as *Cyperus rotundus*, *C. iria*, *C. difformis*, and *Kyllinga brevifolia* Rottb., are excellent examples of weeds that were introduced into the U.S.A. more than a century ago (Elmore, 1984). Likewise, seeds of many annual sedges germinate on the soil surface following a rainfall event without burial, e.g., *C. sanguinolentus* (Carter & Bryson, 2000b). No-tillage or conservation crop production systems tend to favor weeds that germinate from shallow soil depths and perennial weeds. Unless controlled, perennial weeds are an increased problem in reduced-tillage production systems. Difficult-to-control perennial sedges such as *C. esculentus*, *C. rotundus*, and perennial *Kyllinga* Rottb. species often require repetitive and integrated control methods (Bryson & Hanks, 2001). Perennial sedges such as *Cyperus esculentus* and *C. rotundus* and many other perennial weeds regenerate from greater soil depths than most annual weeds (Elmore, 1984; Elmore et al., 1989). Early detection and implementation of control strategies are important in effectively controlling non-native invasive weeds soon after introduction or while still in the lag phase.

Farmers, consultants, and landowners must be ever observant of new weeds and changes within populations of weeds. Weed shifts are inevitable when land use is altered or disturbance occurs. For instance, weed shifts occur in reduced-tillage production systems or where cover crops are utilized (Bryson & Hanks, 2001). Perennial sedges such as *Cyperus esculentus* and *C. rotundus* and many other perennial weeds regenerate from greater soil depths than most annual weeds (Elmore, 1984; Elmore et al., 1989). Likewise, seeds of many annual sedges germinate on the soil surface following a rainfall event without burial, e.g., *C. sanguinolentus* (Carter & Bryson, 2000b). No-tillage or conservation crop production systems tend to favor weeds that germinate from shallow soil depths and perennial weeds. Unless controlled, perennial weeds are an increased problem in reduced-tillage production systems. Difficult-to-control perennial sedges such as *C. esculentus*, *C. rotundus*, and perennial *Kyllinga* Rottb. species often require repetitive and integrated control methods (Bryson & Keeley, 1992; McWhorter & Bryson, 1992; Bryson et al., 1999, 2003b).

In order to assess the impact of a particular weed species effectively, researchers have devised a method to determine the competitive potential of weeds based on field interference studies in agricultural and forest areas (Coble & Byrd, 1992; Reichard & Hamilton, 1997). Interference is ranked among weed species to develop a competitive index or relative competitive abilities table such as the one for selected weeds in cotton created by Coble and Byrd (1992). Such an index aids farmers, consultants, and landowners in determining which species are the most pernicious and helps establish thresholds for the number of weeds that can be tolerated in a given situation. Computerized models (e.g., Soybean Weed Control [SWC] and Mississippi State University Herbicide Application Decision Support System [MSUHADSS]) have been developed to aid farmers
and consultants in making recommendations, which take into account the weed-competitive index, herbicide options and prices, application costs, crop variety (cultivar), row spacing, crop stage, expected weed-free yield potential, expected selling price, soil moisture, and species of weed, population size, and density (Bryson, 2003). However, little research has been conducted to evaluate the thresholds of weeds in natural areas, where populations may far exceed threshold levels before a problem is perceived.

**Identification**

Accurate identification is essential in detecting the presence of weeds and developing the best management strategies for control (Palm et al., 1968; Murray et al., 1992). Traditionally, weed scientists have approached plant identification pragmatically and have adopted simplified systems to be used primarily by individuals with minimal training in systematic botany (e.g., Fischer et al., 1978; Stuckey et al., 1980; Elmore & Bryson, 1986–2001; DeFelice & Bryson, 2004). Such weed identification systems, usually very different from the dichotomous keys commonly used in taxonomic treatments, group weeds by similar susceptibility or resistance to herbicides, effectiveness of cultural-control practices, time of germination, and other factors (Bryson, 2003). In the simplest systems, plants are grouped into general categories (e.g., broadleaved species, grasses, sedges, annuals, or perennials), which is usually sufficient for making decisions about application of broad spectrum and nonselective herbicides. However, the increasing use of more selective herbicides and biological control agents demands greater precision in identification, i.e., determination to specific or infraspecific rank. Among sedges, susceptibility to herbicides is usually correlated with species; however, infraspecific biotypes (e.g., *Cyperus difformis*) do rarely exhibit differential resistance to herbicides (Pappas-Fader et al., 1993, 1994; Hill et al., 1994). In the case of herbicide-resistant biotypes, visual identification is impossible, necessitating the use of bioassays (LeBaron, 1991). Currently, when herbicide resistance is suspected, bioassays are used to determine if the lack of control is due to herbicide resistance, herbicide tolerance, environmental conditions, or misapplication.

Weed scientists and researchers in agriculture usually work with a relatively small subset of all possible plant species in their area, and the agricultural weeds are usually well known. Thus, simplified systems for identification generally work well for most common agricultural weeds. However, when new or unexpected weeds are encountered, more traditional taxonomic methods must be adopted (e.g., use of floristic manuals or systematic treatments in primary literature). Although it may be possible to identify immature sterile specimens of well-known sedges like *Cyperus esculentus* and *C. rotundus*, reliable identification of most sedges to species requires mature fertile specimens and oftentimes the assistance of taxonomic experts. To ensure that the specimen receives proper attention from a taxonomist, it should be prepared using standard methods and should include accurate geographical data (Carter, 2003). To avoid overlooking newly introduced weeds, every effort should be made to collect unfamiliar sedges and to identify them accurately. If one is not able to make a reliable identification, then the specimen with data should be sent to a competent taxonomist for determination. Vigilance, prompt action, and cooperation between plant systematists and weed scientists are absolutely essential in detecting newly introduced sedges and dealing effectively with emerging weed problems. Early detection and rapid response with effective control methods are essential for eradication of non-native invasive weeds (Westbrooks, 1998).

**Factors Determining Competitive Advantage**

The general characteristics of weeds summarized in Table 1 are found to varying degrees in many groups of plants, including sedges. Although no single species exhibits all features, it is presumed that there is usually a direct relationship between the number of these characteristics and the degree of invasiveness of a weed (Radosevich & Holt, 1984; Bryson & Carter, 2004). Most sedges reproduce sexually through the production of large numbers of small achenes. Such small reproductive structures are well suited to both short- and long-distance dispersal. Because of their small size, the achenes of sedges are difficult to detect and are readily transported as contaminants of seeds of crop, lawn, and forage plants. *Cyperus difformis* and *C. iria* are...
major agricultural pests, particularly of rice (Holm et al., 1977). They probably originated as weeds by invading rice paddies in Asia, where they were subject to similar selective pressures as rice. Annual habit, rapid growth, short generation time, high fecundity, and tolerance of submergence of roots have enabled C. difformis and C. iria to persist and disperse as weeds of rice. C. difformis completes its life cycle in just four to six weeks and can go through several generations within a single season (Holm et al., 1977), and an individual plant can produce as many as 50,000 achenes (Jacometti, 1912). These and other sedges are thought to have become naturalized throughout rice-producing areas around the world via dissemination of their achenes as contaminants of rice seed (Bellue, 1932; Muensch, 1955; Kral, 1971).

Obviously, certain characteristics listed in Table 1 are more important as determinants of invasiveness than others. Given the importance of dispersal during the phases of introduction and spread of invasive species (Cronk & Fuller, 1995), characteristics relating to fecundity and dispersal of seeds would be of major importance, as would those providing the ability to spread vegetatively. According to Holm et al. (1977), C. rotundus is the most pestiferous plant in the world. It reproduces and disperses primarily from vegetative tubers, with many biotypes rarely producing viable seeds (Wills, 1987). C. esculentus, also a major agricultural weed, shares similar reproductive characteristics. Vegetative structures such as stolons, rhizomes, and tubers are important in localized spreading of many perennial sedges and may even be transported long distances both naturally and artificially when fragmentation occurs. Subterranean rhizomes, tubers, and corms also enable perennation and survival of sedges during adverse environmental conditions, e.g., cold temperatures, drought, or fire. Further discussion of dispersal in Cyperaceae, including dissemination of vegetative fragments and structural modifications facilitating transport of achenes and other structures, is included below in the Dispersal section.

The highly reduced and inconspicuous flowers of most sedges generally go undetected until after they produce seeds, which Muensch (1955) cited as characteristic of many weeds. Cyperaceae are almost exclusively wind-pollinated (anemophilous). However, entomophily (insect pollination) has been documented to varying degrees in Hypolytrum Rich., Mapania Aubl., Ascolepis Nees ex Steud., Rhynchospora Vahl sect. Dichromena (Michx.) Griseb., Cymophyllus Mack., and even some species of Bolboschoenus (Asch.) Palla, Carex L., Cyperus, and Eleocharis R. Br. (Thomas, 1984a, b; Goetzhebeur, 1998). Although there is a paucity of information, it is suspected that most sedges are cross-pollinated (allogamous). For example, C. esculentus is self-incompatible, and therefore an obligate outcrosser (Brown & Marshall, 1981) with greater genetic variability within sexually reproducing populations than C. rotundus, which rarely produces viable seed (Horak & Holt, 1986; Horak et al., 1987). Cross-pollination in combination with anemophily is thought to contribute to the success of weeds (Baker, 1965, 1974). Some of the most pestiferous sedges are very broadly ranging, exhibiting great infraspecific diversity with many biotypes adapted to a wide variety of environmental conditions. C. rotundus and C. esculentus are cosmopolitan weeds distributed widely throughout the tropics and throughout much of the temperate zone (Kükenthal, 1935–1936). In a worldwide treatment, Kükenthal (1935–1936) recognized numerous infraspecific taxa within these species, indicating considerable adaptation to local environmental conditions.

C$_4$ photosynthesis confers a competitive advantage under conditions of high temperature, high light intensity, and water stress (Hopkins & Hüner, 2004). C$_4$ plants have a lower transpiration ratio, thus, a higher water-use efficiency, than C$_3$ species, brought about by a lower CO$_2$ compensation point, reduced photorespiration, and enzymes (ribulose-1,5-bisphosphate carboxylase [RUBISCO], phosphoenolpyruvate carboxylase [PEPcase]) with higher optimal temperatures (Hopkins & Hüner, 2004). In Cyperaceae, C$_4$ photosynthesis is complex, consisting of four different anatomical types (chlorocycloporoid, rhynchosporoid, fimbristyloid, eleocharoid) and two distinct carbon assimilation modes (Brown, 1975; Soros & Bruhl, 2000). In cladistic analyses using developmental, anatomical, and molecular data, Soros and Bruhl (2000) concluded that C$_4$ photosynthesis arose multiple times (at least four) in the Cyperaceae. Table 2 shows the occurrence of C$_4$ photosynthesis in the genera of cyperaceous weeds. In most cases genera are either C$_3$ or C$_4$; however, five genera, Abildgaardia Vahl, Cyperus, Eleocharis,
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Table 2. The occurrence of C$_3$ and C$_4$ photosynthesis by genus of cyperaceous weeds.$^{1,2,3}$

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<th>Subfamily</th>
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<th>Photosynthetic Pathway</th>
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<tr>
<td>Mapanioideae (13/140)</td>
<td>Mapania (70) C$_3$, Scirpodendron (2) C$_3$, Chrysothricheae (4/13) Lepironia (1) C$_3$</td>
<td>C$_4$[C$_3$]</td>
</tr>
<tr>
<td>Cyperoideae (71/2380)</td>
<td>Eleocharideae (3/200) Eleocharis (200) C$_4$[C$_3$], Abildgaardieae (6/420) Abildgaardia (10) C$_4$[C$_3$], Fimbristylis (300) C$_4$[C$_3$], Bulbostylis (100) C$_4$</td>
<td>C$_4$</td>
</tr>
<tr>
<td>Sclerioideae (15/340)</td>
<td>Sclerieae (1/250) Scleria (250) C$_3$</td>
<td>C$_3$</td>
</tr>
<tr>
<td>Cypereae (19/900)</td>
<td>Cyperus (incl. Anosporum, Juncellus, Mariscus, Torulinium) (550) C$_4$[C$_3$], Kyllinga (60) C$_4$, Queenslandiella (1) C$_4$, Pycreus (100) C$_4$, Lipocarpha (35) C$_4$, Oxyccaryum (1) C$_3$, Isolepis (60) C$_3$, Courtoisina (2) C$_3$ Schoeneae (29/700) Rhynchospora (250) C$_3$[C$_4$], Cladium (4) C$_3$, Lepidosperma (55) C$_3$</td>
<td></td>
</tr>
</tbody>
</table>


$^2$ Subfamily and tribal classification and numbers of genera and species in parentheses are from Goetghebeur (1998).

$^3$ Authority names for genera in Table 2 not discussed elsewhere in this paper are as follows: Actinoscirpus (Ohwi) R. W. Haines & Lye; Cyperus sect. Anosporum (Nees) Pax.

Fimbristylis Vahl, and Rhynchospora have both C$_3$ and C$_4$ species. Of these, the mostly aquatic to subaquatic Eleocharis is almost entirely C$_3$, and all of the subgenera of Cyperus are C$_4$ except Pycnostachys C. B. Clarke [= Protocyperus]. Although many weeds are not, some of the most competitive are characterized by C$_4$ photosynthesis (Black et al., 1969; Elmore & Paul, 1983). Holm et al. (1977) rank C. rotundus, C. esculentus, C. difformis, and C. iria among the world’s worst weeds. Cyperus rotundus, C. esculentus, and C. iria are C$_4$ plants; C. difformis is C$_3$ (Hesla et al., 1982). Because C$_4$ photosynthesis is only one of many factors contributing to the competitiveness of weeds (Baskin & Baskin, 1978), it is not surprising that other characteristics enable certain C$_3$ Cyperaceae to be highly competitive weeds. C$_4$ photosynthesis is normally most advantageous in the terrestrial environment under conditions of drought, high light, and high temperatures (Hopkins & Hüner, 2004). Cyperus difformis is almost exclusively a pest of rice and is well adapted to aquatic environments, where excessive water in the environment ameliorates high temperatures, and water stress is normally not a factor. Thus, it is not surprising that C. difformis has C$_3$ photosynthesis. Similarly, the C$_3$ species C. haspan is a major weed of rice agriculture.

Although data on photosynthetic pathways for most species of cyperaceous weeds are lacking, generic-level data for species listed in Appendix 2 indicate a predominance of weeds in genera that are exclusively or primarily C$_4$ (Fig. 1). Thus, it appears that C$_4$ photosynthesis has been a major factor in the success of genera such as Cyperus, Fimbristylis, Kyllinga, and Bulbostylis DC. as weeds.

Certain plants, including weeds, achieve a competitive advantage through allelopathy, the production of chemical compounds that suppresses seed germination and growth in competing plants. Allelopathy is
well known in *Cyperus rotundus* and *C. esculentus* and has been cited as a factor in its competition with cotton and other crops (Friedman & Horowitz, 1971; Mallik & Tesfai, 1988; Martinez-Diaz, 1997). Although it has not been investigated, the nearly monotypic nature of invasive populations of *C. enterrianus*, observed in southern Louisiana and eastern Texas, U.S.A. (Carter, 1990; Carter & Bryson, 1996), suggests an allelopathic effect.

Weeds may also harbor insects and pathogens that adversely affect agricultural crops and native plants (USDA, 1960; Tietz, 1972). *Cyperus dives* Delile, the natural host for a moth (*Eldana saccharina* Walker) whose larvae cause losses to the sugar industry, is of some concern as a weed in southern Africa, where it is native and where an increase in its frequency is associated with clearing of natural vegetation for the cultivation of sugarcane (Gordon-Gray, 1995). *Cyperus papyrus* L. is also thought to harbor this same moth (Gordon-Gray, 1995). Noctuid moth larvae of *Spodoptera frugiperda* (J. E. Smith) [= *Laphygma frugidera* (Abbott & Smith)] reportedly feed on *C. rotundus*, *Carex* spp., barley (*Hordeum vulgare* L.), cotton, milo (*Sorghum bicolor* (L.) Moench.), potato (*Solanum tuberosum* L.), rice, soybean, sweet potato, and other crops and native plant species (Tietz, 1972). *Colletotrichum graminicola* (Ces.) G. W. Wils., a fungal pathogen, infects *Carex* spp., other Cyperaceae, and grass crops (USDA, 1960). *Cyperus esculentus*, *C. rotundus*, chili peppers (*Capsicum annuum* L.), and other crops are hosts to the southern root-knot nematode (*Meloidogyne incognita* (Kofoid & White) Chitwood) (Schroeder et al., 1993).

**Dispersal**

Dispersal is fundamentally important in determining distributional patterns of plant species. Dispersal may be complex and dynamic involving both sexual and asexual systems, multiple vectors, and shifts in vectors. When released from competition, predation, and disease, many species, upon introduction outside their natural ranges, have potential to become weeds. Dispersal is crucial at two points during invasion by plants: first, during the initial introduction of the species and later, after naturalization, as the invasive species spreads, expanding its range (Cronk & Fuller, 1995). Consequently, basic knowledge about attributes of reproduction and natural dispersal can provide insight into which species are likely to become invasive weeds and how they might be dispersed.

Vegetative growth from rhizomes, stolons, runners, tubers, and corms is common in many perennial sedges and is undoubtedly very important in local expansion. Some species, e.g., *Eleocharis melanocarpa* Torr., *E. microcarpa* Torr., and *E. rostellata* Torr., have arching aerial stems that take root apically upon contact with the ground, and others, like *E. vivipara* Link, proliferate vegetatively from spikelets. *Cyperus pectinatus* Vahl forms plantlets vegetatively from its inflorescence (Haines & Lye, 1983). Vegetative growth when coupled with fragmentation and transport of asexual propagules can also result in more distant dispersal. This is perhaps most effective in the dispersal of fragments broken from rafts (sudds) of floating or submerged natant aquatic sedges by water currents or wind. Such dispersal has been noted in *C. cephalotes* Vahl, *C. colymbetes* Kotschy & Peyr., *C. mundtii* Kunth, *C. papyrus*, *C. pectinatus*, and *Oxyacrium cubense* (Poep. & Kunth) Palla (Kern, 1974; Haines & Lye, 1983; Gordon-Gray, 1995). We have noted this phenomenon in *C. alopecuroides* Rottb., *C. prolifer* Lam., *Eleocharis baldwinii* (Torr.) Chapm., *E. vivipara*, and *O. cubense* and suspect that it occurs in other species similar in habit and habitat, e.g., *C. elatus* L. and *Websteria confervoides* (Poir.) S. S. Hooper (Kern, 1974).

Sedges exhibit a variety of modifications exploiting various agents of dispersal, most of which directly involve fruits or inflorescences. A number of mechanisms involving dispersal of achenes by wind (anemochory) are known in Cyperaceae. In *Afrotrolepis* (Gilly) J. Raynal, *Carpha* Banks & Sol. ex R. Br., *Costularia* C. B. Clarke, *Eriophorum* L., and *Scirpus* L., a persistent perianth adnate to the achene is modified into long, silky bristles or hairs that facilitate transport by wind (Kern, 1974; Pijl, 1982; Haines & Lye, 1983; Goetghhebeur, 1998), and in *Androtrichum* Brongn. and *Machaerina* Vahl, persistent elongated filaments have the same function (Goetghhebeur, 1998). Also, the flattened wing-like floral scales of *Anosporum* spp. and the flattened winged spikelets of certain *Kyllinga* spp. (Haines & Lye, 1983) promote wind dispersal of the achenes retained within. Such dispersal of spikelets has been
observed over short distances during collection of specimens of the introduced weed *K. squamulata* Thonn. ex Vahl (Carter, pers. obs.).

Dispersal by water (hydrochory) is well documented in Cyperaceae. The fruits or spikelets of most terrestrial sedges are disseminated to some extent by rain; however, such dispersal is usually quite local (Ridley, 1930). The achenes of the aquatic and wetland sedges *Cyperus* (Anosporum) *colmabetes*, *C. pectinatus*, *C. platystylis* R. Br., *Oxycaryum cubense*, several *Scirpus* spp., and certain wetland *Carex* spp. have a spongy suberized pericarp that facilitates flotation and dispersal by moving water (Chermezon, 1924; Ridley, 1930; Kern, 1974; Lye, 1981; Haines & Lye, 1983). Achenes of *Cladium* P. Browne were observed to float in the laboratory for up to 15 months (Ridley, 1930). Similarly in *Cyperus odoratus* L. and *Remirea maritima* Aubl., the achene remains enclasped in a buoyant corky rachilla and is thereby dispersed by moving water (Kern, 1974; Haines & Lye, 1983). Floods undoubtedly transport even unmodified, nonbuoyant achenes, vegetative fragments of plants (e.g., rhizomes, tubers), and whole plants (Kern, 1974) and deposit them far from the main channel along basins of major rivers. *Cyperus fuscus* L., a potential rice weed in the U.S.A., has apparently been dispersed by floodwaters along the Missouri River in the central U.S.A. (McKenzie et al., 1998).

Dispersal of achenes by animals (zoochory), especially birds, is important in Cyperaceae. Zoochory may involve the internal (endozoic) transport of achenes within the digestive system or external (epizoic) transport. The achenes of *Carex*, *Cladium*, *Cyperus*, *Fimbristylis*, *Rhynchospora*, and *Scirpus* have been identified in the alimentary systems of waterfowl (Ridley, 1930). Waterfowl and other birds consume large quantities of achenes,
especially of *Cyperus* spp. and *Eleocharis* spp., and their endozooic transport plays an important role in dispersal of sedges over long and short distances (Ridley, 1930; Kern, 1974; Haines & Lye, 1983). Vlaming and Proctor (1968) experimentally determined that sedge achenes remained viable after retention in avian digestive systems for periods up to 120 hours: *Cyperus ochraceus* Vahl, max. 37 hr.; *Eleocharis albida* Torr., max. 38 hr.; *E. macrostachya* Britton, max. 77 hr.; *E. parvula* (Roem. & Schult.) Link ex Bluff, Nees & Schauer max. 30 hr.; and *E. quadrangulata* (Michx.) Roem. & Schult., max. 120 hr. Brightly colored fruits in the tropical genus *Gahnia* J. R. Forst. & G. Forst. are consumed and dispersed by birds (Benl, 1937; Pijl, 1982; Lye, 2000), and, according to Sauer (1988), seeds of *Carex nigra* (L.) Reichard were brought to Iceland by snow bunting from Great Britain. Short-distance endozoic dispersal by cattle (*Carex, Scirpus*) and water buffalo (*Fimbristylis globulosa* Retz.) Kunth, *F. littoralis* Gaudich.) has been reported by Kern (1974).

Similarly, the epizoic transport of achenes in mud adhering to the feet of migratory waterfowl is implicated in long-distance dispersal in *Cyperus, Eleocharis, Rhynchospora*, and *Scirpus* (Ridley, 1930; Kern, 1974). Such mechanisms could account in part for the wide distributions of *C. drummondii* Torr. & Hook., *C. odoratus*, *C. virens* Michx., and *Oxycaryum cubense*. A number of epizoic mechanisms involving various structural modifications are known in Cyperaceae. The achenes of many species of *Eleocharis, Fuirena* Rothb., *Rhynchospora, Schoenoplectus* (Rchb.) Palla, and *Websteria* S. H. Wright are subtended by persistent, hypogynous bristles beset with retrorse barbs that readily attach to feathers or hair of animals (Kern, 1974; Haines & Lye, 1983), and the North American sedge, *C. plkenetii* Fernald, exhibits a number of modifications that facilitate dispersal of intact spikelets by attachment to animal hair (Carter, 1993). *Uncinia* Pers., widely distributed in the Southern Hemisphere, including many islands of the Pacific, is characterized by a hooked inflorescence axis that extends beyond the utricle, attaching readily to feathers and enabling transport by birds (Pijl, 1982; Mabberley, 1997). *Carex pauciflora* Lightf. has a springing mechanism that disperses its perigynia over relatively short distances when touched by animals (Hutton, 1976), and the perigynia of certain other *Carex* spp. produce oil-rich appendages and are dispersed by ants (Handel, 1976, 1978; Gaddy, 1986). Similarly, a fleshy perianth in *Lepidosperma* Labill. reportedly facilitates dispersal by ants (Goetghbeuer, 1998).

High fecundity and small fruits (achenes) make sedges especially susceptible to unintentional dissemination directly by humans or through their activities. A variety of human activities are known or suspected to disperse sedges, and most of these involve movement of their small, inconspicuous achenes. Sedge achenes are readily dispersed as contaminants of commercial seed supplies (Koyama, 1985; Bryson & Carter, 1992; Sell & Murrell, 1996), and achenes or even live plants may contaminate ornamental nursery stock, potted plants, or mulch. A number of sedges associated with rice agriculture around the world (cf. *Bolboschoenus, Cyperus, Eleocharis, Fimbrystylis, Schoenoplectus* in Appendix 1) are thought to have dispersed via achenes as contaminants of rice seed (Bellue, 1932; Muensch, 1955; Kral, 1971). Shipments of shorn wool may contain achenes of sedges, which when dispersed result in the introduction of so-called “wool aliens” (Sell & Murrell, 1996). Other kinds of cargo, including live animals, transported by land, sea, or air may harbor achenes resulting in the unintentional introduction of sedges (Carter & Mears, 2000). Dumping of ballast contaminated with achenes or vegetative propagules (e.g., rhizomes, stolons, tubers) has long been associated with dispersal of sedges and other plants (e.g., Smith, 1867; Brown, 1880; Britton, 1886; Mohr, 1901). The inadvertent transport of achenes or vegetative propagules embedded in mud or lubricants adhering to wheels or other parts of freight cars, trucks, automobiles, and airplanes undoubtedly disperses sedges, and migration of plants, including sedges, along railroads (ferroviiatic migration) is well documented (e.g., Mühlenbach, 1979, 1983). It also seems likely that tiny achenes of sedges, drawn by jet airplane engines, could lodge in the housing of the engine or other parts and be carried great distances. The transport of turfgrass sod, mulch, soil, hay, and fodder has been associated with dispersal of sedges, e.g., *Cyperus esculentus*, *C. rotundus*, *Kylinga brevifolia*, and *K. gracillima* Miq. (Bryson et al., 1992b, 1996, 1997; Sell & Murrell, 1996), and movement of achenes and vegetative propagules occurs during construction and maintenance of roads, e.g., *Cyperus enterianus*, *C. sanguinolentus*, *Carex oklahomensis* Mack., and

Because sedges are generally inconspicuous, and other than as weeds are of minimal economic importance, they escape all but casual notice and interest of most humans; consequently, it is presumed that the intentional dispersal of sedges by humans is infrequent. However, as shown in Appendix 1 and in Figures 2 and 3, there is an increased interest in using sedges as ornamentals, and a surprising number of species are subject to deliberate transfer by humans. Some of these have become naturalized weeds from cultivation, and any could potentially become pests. Carex comans Berggr., C. morrowii Boott, C. pendula Huds., C. riparia Curtis, Cymophyllus fraserianus (Ker Gawl.) Kartesz & Gandhi, Cyperus compressus L., C. eragrostis, C. longus L., C. owanii Boeckeler, and C. strigosus L. are used in gardens, and Carex bacans Nees, Cyperus albostratius Schrad., C. fertilis Boeckeler, and Isolepis cernua (Vahl) Roem. & Schult. are sometimes used as potted plants or in hanging baskets (Bailey, 1935, 1949; Bailey & Bailey, 1976; Everett, 1980–1982; Brickell & Zuk, 1997). Of these, Carex riparia, Cyperus compressus, C. eragrostis, and C. longus are listed as weeds (cf. Appendix 2), and the South African C. owanii is naturalized, but apparently not invasive, in California, U.S.A. (Tucker et al., 2002).

Cyperus alternifolius L. subsp. flabelliformis Kük. (umbrella plant, umbrella sedge) has been used as an ornamental in water gardens and as a potted plant for more than 200 years (Bailey & Bailey, 1976). It is widely naturalized from cultivation throughout the tropics and subtropics (Kern, 1974; Koyama, 1985) and is frequently cited as a weed (cf. Appendix 2). Other sedges cultivated in water gardens include C. papyrus (papyrus), C. prolifer (dwarf papyrus, miniature papyrus), C. sexangularis Nees, C. textilis Thunb., and various bulrushes, Bolboschoenus robustus (Pursh) Soják, Schoenoplectus acutus (Muhl. ex J. M. Bigelow) Á. Löve & D. Löve, S. heterochaetus (Chase) Soják, S. tabernaemontani (C. C. Gmel.) Palla, S. lacustris (L.) Palla, and Scirpus cyperinus (L.) Kunth (Bailey, 1935, 1949; Everett, 1980–1982; Gordon-Gray, 1995). Cyperus papyrus is naturalized in Australia (Wilson, 1993) and in Florida, U.S.A. (Wunderlin, 1998), and C. prolifer is naturalized in Florida (Carter et al., 1996).

Appendix 1 is a list of sedges known or suspected to be transported by human activities. The frequencies of various modes of anthropogenic dispersal in Cyperaceae are shown in Figure 2: ornamentals (53%); wool aliens (13%); ballast (7%); rice agriculture (7%); revegetation, reclamation, erosion control, and soil improvement (7%); and highways and railroads (3%). The burgeoning human population and the current ease and frequency of rapid long-distance transportation of humans and cargo make it inevitable that such dispersal of sedges, both unintentional and deliberate, will continue into the foreseeable future.

**Invasion by Cyperus entrerianus: A Case Study**

The following case study of Cyperus entrerianus (deeprooted sedge), based upon Carter (1990) and subsequent investigation (Carter, unpubl. data), shows how basic research in the field and the herbarium allows for the detection of invasive weeds and illustrates the need for accurate and timely identification in order to take appropriate action against them. In 1987, Carter found a species of Cyperus in Ware County, Georgia, that did not fit any descriptions of species known from the southeastern U.S.A. During 1988 and 1989, intensive searching in the field resulted in discovery of numerous additional populations of this perplexing sedge in Florida, Georgia, Alabama, Louisiana, and eastern Texas. During this same period, an examination of herbarium specimens at FSU, IBE, and VDB revealed additional ones, variously misidentified, that were collected from northern Florida in the 1970s and 1980s, southern Louisiana in 1975, and eastern Texas in 1981. In early 1989, Carter correctly determined that the enigmatic sedge was C. entrerianus.

Based upon data gleaned from herbarium specimens and intensive field research and Rosen et al. (2006), the following hypothetical scenario for the introduction, naturalization, and dispersal of Cyperus entrerianus in the U.S.A. is proposed (Fig. 4). Cyperus entrerianus was introduced into the U.S.A. before 1941, and the suspected points of introduction are Cameron County, Texas, and Pensacola, Florida (Brinker 413, US). The species was not found again in
the U.S.A. until 1974, when it was collected again in Pensacola (Godfrey 73755, FSU). It was collected in southern Louisiana in 1975 (Allen 6674, VDB), additional collections were made in Escambia and Gulf counties, Florida, during the late 1970s and 1980s, and it was found in eastern Texas in 1981 (Carter, 1990). All of the collections of *C. entrerianus* made by others before it was reported new to the U.S.A. by Carter (1990) were variously misidentified as *C. pseudovectatus* Steud., *C. robustus* Kunth, *C. virens*, and *C. virens* var. *drummondii* (Torr. & Hook.) Kük. The paucity of herbarium records before the mid-1980s suggests that *C. entrerianus* was in its lag phase until then. Although the apparent rapid expansion of range in the late 1980s and 1990s is undoubtedly in part an artifact of intensive searching for *C. entrerianus* by Carter and others (Carter, 1990; Carter & Jones, 1991; Bryson & Carter, 1994; Carter & Bryson, 1996), its collection at a number of sites in Louisiana and Florida during the later 1970s by researchers who had no knowledge of its correct identity indicates that its lag phase had ended some years earlier.

It is suspected that *Cyperus entrerianus* was introduced independently in southern Texas and at Pensacola from temperate South America or Mexico (Carter, 1990; Rosen et al., 2006). There are other cases of introduced *Cyperus* weeds that were probably imported into Pensacola via ballast: *C. aggregatus* (Willd.) Endl., *C. difformis*, *C. pilosus* Vahl, and *C. reflexus* Vahl (Burkhalter, 1985; Wunderlin, 1998); thus, introduction of *C. entrerianus* via ballast is plausible. Distribution and habitat indicate that *C. entrerianus* has spread from its point of introduction at Pensacola via dispersal from road construction and maintenance activities, primarily along highway Interstate 10 and secondarily along intersecting highways (Carter, 1990; Carter & Bryson, 1996). It is probably also now dispersed endozoically by birds or other animals that consume its achenes. Certain populations of *C. entrerianus* in the southeastern U.S.A. show evidence of introgression with *C. surinamensis* Roth., which could account in part for the robust habit (heterosis) observed in plants there (Carter, 1990). Vigorous growth and robust form have probably facilitated the rapid expansion of *C. entrerianus* in the southeastern

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**Figure 2.** Percentages of various kinds of anthropogenic dispersal of cyperaceous weeds listed in Appendix 1.
U.S.A. from Florida and southern Georgia west into eastern Texas, and it has begun to invade natural areas in eastern Texas (Rosen et al., 2006).

**Survey of Genera and Selected Species**

There is no comprehensive, contemporary, cosmopolitan enumeration and description of species of Cyperaceae, and such comprehensive accounts of most cyperaceous genera do not exist. Furthermore, there is still considerable disagreement about taxonomic limits and circumscriptions of many genera. Consequently, estimates of numbers of taxa (genera/species) vary considerably: ca. 70/ca. 4000 (Cronquist, 1981); 98/4350 (Mabberley, 1997); 104 genera/5000+ (Goetghebeur, 1998); ca. 100/ca. 5000 (Ball et al., 2002). For example, there is little consensus about the circumscription of *Cyperus*, i.e., whether it should be defined broadly to include *Diclidium* Schrad. ex Nees, *Juncellus* C. B. Clarke, *Kyllinga*, *Mariscus* Vahl, *Pycreus* P. Beauv., and *Queenslandiella* Domin with infrageneric rank, or whether it should be defined narrowly with the segregates treated as genera. This problem has major implications with respect to nomenclature in *Cyperus*, the most important genus of weeds in the family (Carter & Bryson, 2000a). Use of molecular techniques (e.g., Muasya et al., 2000a, b) should help to stabilize nomenclature by resolving the taxonomic status and rank. However, until such basic problems are resolved through additional research and alignment of nomenclature, we think a conservative approach is warranted. Herein where possible, nomenclature at the generic level follows the recently published *Flora of North America*, volume 23. However, in the absence of a synonym under *Cyperus*, one species, *Pycreus decumbens* T. Koyama, reported as a weed in Brazil by Kissmann (1997), was not listed in Appendix 2. *Cyperus decumbens* Govind., the name for a different species from India published in 1973, prevents legitimate transfer of the name under *Cyperus*.

Based upon a survey of more than 60 publications, Appendix 2 is a worldwide list that includes 449 species of Cyperaceae that have been cited as weeds. Additionally, we have included other sedges indigenous to the southeastern U.S.A. that we have observed to be weeds. Table 3 summarizes numbers of weedy species by genus. *Cyperus* is by far the

![Figure 3. Cumulative numbers of ornamental and cultivated species of Cyperaceae listed in selected horticultural references from 1935 to 2001.](image-url)
Rhynchospora, Kyllinga, Bulbostylis, Fuirena, Scirpus, and Bolboschoenus had fewer than 5% each, and the remaining 10 genera had fewer than 1% each. Cyperaceae, which includes Cyperus, is the largest tribe of weeds (Fig. 5), and subfamily Cyperoideae, which includes Cyperaceae, has the overwhelming majority of weedy sedges (Fig. 6).

The previous lists of Holm et al. (1977, 1979, 1997) and WSSA (1989) show a substantially larger proportion of weeds in Cyperus (ca. 42%); ca. 43% in Eleocharis, Fimbristylis, Scirpus (incl. Bolboschoenus, Isolepis R. Br., Schoenoplectus); and the remaining 15% in Carex, Cladium, Fuirena, Kyllinga, Rhynchospora (incl. Dichromena, Psilocarya Torr.), and Scleria. Our survey (Appendix 2) shows a much smaller proportion in Cyperus and substantial increases in Carex and other genera. Bayer AG (1992) was not used in compiling Appendix 2 because it does not separate weeds from crops and because it is based upon key sources cited in Appendix 2.

**ABILDGAARDIA**

Abildgaardia is a genus of ca. 15 species distributed mostly in the tropics and subtropics in both the Eastern and Western hemispheres (Kral, 2002d). Although Abildgaardia spp. have been placed in Bulbostylis and Fimbristylis, embryological and anatomical data support segregation as a separate genus (Lye, 1973). The results of our survey (Appendix 2) show only one species, *A. ovata* (Burm. f.) Kral, cited as a weed, which is reported to be a weed in Asia, North America, and the Pacific Islands (Holm et al., 1979). In southern Florida, U.S.A., it is occasionally a weed of gravelly soils in waste areas, along highways, and in lawns (Carter, pers. obs.).

**BOLBOSCHOENUS**

Bolboschoenus is a genus of 6 to 15 species (Smith, 2002a), five of which are listed as weeds in Appendix 2. *Bolboschoenus maritimus* (L.) Palla, considered among the world’s worst weeds, is a pest in agricultural lands and waterways in Africa, Asia, Australia, Europe, and North and South America (Holm et al., 1997; Kissmann, 1997). It is a troublesome rice weed in paddy fields (Holm et al., 1977, 1997), and in the southern Korean peninsula *B. maritimus* infests more than 80% of rice fields reducing yields by as much as 50% when adequate control
measures are not taken (Ryang et al., 1978). Integrated weed management schemes, including rotation of crops, water regimes, and chemical and cultural methods, effectively control B. maritimus in rice-producing areas of Asia (De Datta & Jereza, 1976; Verga et al., 1977). Bolboschoenus fluviatilis (Torr.) Sojak is reported as an aquatic weed in Asia, Australia, and North America (Holm et al., 1979; WSSA, 1989).

Table 3. Numbers and percentages of cyperaceous weeds by genus (data extracted from Appendix 2).

<table>
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<tr>
<th>Genus</th>
<th>Species (infrasp.)</th>
<th>Percent of Total</th>
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</thead>
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<tr>
<td>Cyperus¹</td>
<td>147 (2)</td>
<td>33</td>
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<tr>
<td>Carex</td>
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<td>Abildgaardia</td>
<td>1</td>
<td>&lt; 1</td>
</tr>
<tr>
<td>Courtoisina</td>
<td>1</td>
<td>&lt; 1</td>
</tr>
<tr>
<td>Isolepis</td>
<td>1</td>
<td>&lt; 1</td>
</tr>
<tr>
<td>Lepidosperma</td>
<td>1</td>
<td>&lt; 1</td>
</tr>
<tr>
<td>Lepironia</td>
<td>1</td>
<td>&lt; 1</td>
</tr>
<tr>
<td>Mapania</td>
<td>1</td>
<td>&lt; 1</td>
</tr>
<tr>
<td>Oxycaryum</td>
<td>1</td>
<td>&lt; 1</td>
</tr>
<tr>
<td>Scirpodendron</td>
<td>1</td>
<td>&lt; 1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>449 (2)</strong></td>
<td><strong>100</strong></td>
</tr>
</tbody>
</table>

¹ Includes Diclidium, Juncellus, Mariscus, Pyreus, and Queenslandiella.

of B. maritimus are readily dispersed by birds (Holm et al., 1997) and by water (Guppy, 1893). B. fluviatilis is less a problem in the equatorial zone than in semitropical and temperate regions of the world (Holm et al., 1997). The achenes of B. maritimus are readily dispersed by birds (Holm et al., 1997) and by water (Guppy, 1893). B. fluviatilis is less a problem in the equatorial zone than in semitropical and temperate regions of the world (Holm et al., 1997). The achenes

BULBOSTYLIS

Bulbostylis is a genus of ca. 100 species, occurring mostly in dry or periodically dry, sunny, sandy uplands and savannas in warm temperate and tropical regions worldwide (Kral, 2002c). Nine species are listed as weeds in Appendix 2; however, none is a major weed. Bulbostylis barbata (Rottb.) C. B. Clarke and B. capillaris (L.) C. B. Clarke are occasionally weeds of sandy soil in flowerbeds and poorly managed turf in the southeastern U.S.A. In late summer and fall in the Coastal Plain of the southeastern U.S.A., B. barbata can be a conspicuous feature of the landscape when en masse its reddish brown inflorescences appear in sandy cultivated fields (Kral, 1971). Bulbostylis capillaris and B. ciliatifolia (Elliott) Fernald are common weeds of sandy fallow fields, roadsides, and on gravel and cinders of railroad right-of-ways (Kral, 1971; Godfrey & Wooten, 1979). All three species often grow in sandy soil in flowerbeds and lawns or through cracks in sidewalks and parking lots. Bulbostylis barbata is reported as a weed of cultivated lands in Taiwan (Lin, 1968), and B. capillaris is reported as a weed in Brazil (Kissmann, 1997).

CAREX

Of the more than 2000 species worldwide (Ball & Reznicek, 2002), only a small proportion of Carex spp. are major weeds when compared to other sedge groups (e.g., Cyperus, Kyllinga). Although not among the most troublesome weeds of rice, Carex diandra Schrank and C. pycnostachya Kar. & Kir. are reported from rice field habitats in Pakistan (Kukkonen, 2001). Very few Carex spp. are invasive, and none is a principal agricultural weed (Holm et al., 1977), which may be due to several factors including more restrictive habitat requirements, fewer or larger seeds, shorter period of sexual reproduction, fewer vectors for dispersal, lack of tolerance to mowing or tillage, and greater susceptibility to herbicides. In Appendix 2, 82 species of Carex are listed as weeds.
**Carex blanda** Dewey and **C. leavenworthii** Dewey are occasional weeds of poorly kept lawns, especially under shade of deciduous trees in the southeastern U.S.A. (Bryson, 1985a). **Carex blanda** is often locally abundant and capable of being weedy in diverse environmental and edaphic conditions (Bryson & Naczi, 2002). It is highly likely that **C. blanda** and other weedy **Carex** species are dispersed as contaminants of grass seed, sod, or clippings for turf establishment (Jones et al., 1993). In lawns and on golf courses, **C. blanda** and **C. leavenworthii** are controlled by frequent mowing and herbicide treatments (Bryson, 1985a). Listing of **C. cephalophora** Muhl. ex Willd. as a weed (Callahan et al., 1995) may be due to taxonomic confusion with **C. leavenworthii** and literature that considered the two taxa conspecific. Another occasional lawn weed, **C. cherokeensis** Schwein., is a weed of pastures (Burns & Buchanan, 1967; Burns et al., 1969; Bryson, 1985a). In the Black Prairie and Lower Coastal Plains regions of Alabama, **C. cherokeensis** is reported to displace desirable forage species in poor quality pastures (Burns & Buchanan, 1967; Burns et al., 1969). **Carex cherokeensis** persists and spreads in the early spring or late fall by extensive rhizomes when many pasture grasses are dormant. It is more prevalent in poorly managed pastures lacking herbicide applications, and mowing alone is not effective in **C. cherokeensis** control.

**Carex longii** Mack. is weedy along roadsides and in lawns and flowerbeds (Bryson, 1985a). Unlike most **Carex, C. longii** flowers and fruits throughout the frost-free months. Frequently in the southeastern U.S.A., establishment of this species occurs following dispersal of pine bark mulch around shrubs and in flowerbeds suggesting contamination by **C. longii** seeds. From flowerbeds, **C. longii** can invade surrounding areas; however, it is not as aggressive as several invasive **Cyperus** and **Kyllinga** spp. in lawns, turf, gardens, and row crops (Bryson, pers. obs.). Listing of **C. albolutescens** Schwein. as a weed (WSSA, 1989) may be due to taxonomic confusion recently clarified by Rothrock (1991). Although **C. albolutescens** may be locally common, it is not weedy along roadsides and in lawns, pastures, and flowerbeds like **C. longii**.

Non-native **Carex** species have become invasive weeds in natural areas through accidental introduction or escape from cultivation as ornamentals. On sandy beaches and dunes, **C. kobomugi** Ohwi, native to Japan, has become an invasive weed along Atlantic coasts (Standley, 1983). It was first collected in the U.S.A. in 1929 (Fernald, 1930), but at that time, it was misidentified as the closely related species **C. macrocephala** Willd. ex Spreng. Since 1929, **C. kobomugi** has spread on sandy beaches from Rhode Island southward to North Carolina and displaced native vegetation and altered the structure of beaches (Small, 1954; Svenson, 1979; Stalter, 1980; Standley, 1983). Its range is likely to expand (Mastrogiuseppe, 2002) despite current eradication efforts in several states. Following introduction as an ornamental, **C. pendula** has recently escaped into natural areas and is beginning to appear on roadsides and stream banks; however, its potential as an invasive weed is unknown (Reznicek, 2002).

Some **Carex** species native to one region of a continent have become weedy in other regions of the same continent. Northern and eastern records of **C. oklahomensis** are most recent, and this sedge may be increasing its range (Standley, 2002). Because **C. oklahomensis** has been frequently collected from recently completed construction sites, it is probably dispersed in hay mulch used for erosion control along roadsides, lakesides, and ditch banks (Bryson et al., 1992a, 1996). **Carex opaca** (F. J. Herm.) P. Rothr. & Reznicek appears to be similarly dispersed (Bryson et al., 1994b).

Seeds and rhizomes of **Carex praegracilis** are dispersed along highways by traffic and by construction and maintenance equipment, and it is sometimes called “tollway sedge” or “freeway sedge” (Swink & Wilhelm, 1979; Bruton & Catling, 1982). **Carex praegracilis** is adapted to extreme environmental conditions (e.g., salty or dry roadsides) and is spreading rapidly eastward and southward from its native range, especially along roadsides where salt is applied for deicing (Reznicek et al., 1976; Bruton & Catling, 1982; Cusick, 1984; Reznicek & Catling, 1987, 2002).

**Carex nebrascensis** Dewey is listed as a weed (WSSA, 1989; Callahan et al., 1995); it was apparently introduced into Missouri and Illinois, U.S.A., and has become weedy along roadsides (Standley et al., 2002). Heavy infestations of **C. lanuginosa** Michx. were effectively controlled by herbicides, and tillage provided better control of this sedge in light (sandy) soils than in heavier (silt or clay) soils in New Mexico, U.S.A. (Hollingsworth, 1969).

**CLADISM**

There are four species of Cladium worldwide with three in North America (Tucker, 2002a), of which two, C. jamaicense Crantz and C. marisoides (Muhl.) Torr., are cited as weeds (Holm et al., 1979; WSSA, 1989). Both of these wetland species occur in the U.S.A. Cladium jamaicense (saw grass) inhabits marshes near the coast and is the predominant species of the Everglades marshes of southern Florida, U.S.A. (Steward & Ornes, 1975; Godfrey & Wooten, 1979). Much of this formerly vast marshland has been drained for flood control and converted into agricultural fields for the cultivation of sugarcane and other crops (Godfrey & Wooten, 1979). In such an altered and unnatural landscape, C. jamaicense is viewed as an impediment to drainage and navigation and a hindrance to agriculture.

![Figure 5. Number of cyperaceous weeds by tribe; classification follows Goetghebeur (1998).](image-url)
However, a massive venture is currently underway (U.S. Army Corps of Engineers, 1999) to reverse the damage done by drainage projects of the past and to reclaim portions of the Everglades ecosystem, which if successful will also restore the natural habitat of $C. jamaicense$, taking it from weed to its former status as the predominant plant of its natural community. Weediness is oftentimes an artifact of human perception and folly.

**COURTOISINA**

*Courtoisina* Soják is a small genus of two species found in Africa, Madagascar, India, and southeastern Asia (Haines & Lye, 1983; Gordon-Gray, 1995; Vorster, 1996; Mabberley, 1997). *Courtoisina cyperoides* (Roxb.) Soják was cited as a weed in rice fields (Simpson & Koyama, 1998; Simpson & Inglis, 2001) and has also been reported from wet mud of freshwater pans, seasonally wet grasslands, and temporary pools (Haines & Lye, 1983; Gordon-Gray, 1995).

![Figure 6. Number of cyperaceous weeds by subfamily; classification follows Goetghebeur (1998).](image)

There are about 600 species of *Cyperus* worldwide (Tucker et al., 2002). In terms of their significance as weeds, *Cyperus* species are by far the most important in Cyperaceae. Appendix 2 lists 147 species of *Cyperus* that have been cited as weeds. The adverse economic impact of *Cyperus* is great. According to Holm et al. (1977), it contains the world’s worst weed and three additional species listed among the 33 worst agricultural weeds in the world. The most recent comprehensive, universal treatment of *Cyperus* was by Kükenthal (1935–1936), who defined the genus broadly as consisting of six subgenera: *Cyperus*, *Mariscus* (Vahl) C. B. Clarke, *Torulinium* (Desv.) Kük., *Juncellus* (C. B. Clarke) C. B. Clarke, *Pycreus* (P. Beauv.) A. Gray, and *Kyllinga*. *Cyperus* is taxonomically complex, and the status of its subgenera is widely disputed even among contemporary workers (cf. Kern, 1974; Haines & Lye, 1983; Koyama, 1985; Lye, 1992; Wilson, 1993; Adams, 1994; Gordon-Gray, 1995;
Muasya et al., 2000a, b, 2002; Tucker et al., 2002). Although we question the apparent inconsistency in segregating *Kyllinga* and not *Pycreus* and *Juncellus*, herein we pragmatically adopt the generic taxonomy in *Flora of North America*, Vol. 23 (Tucker et al., 2002). Recent molecular evidence seems to support a broad circumscription of *Cyperus* to include *Kyllinga*, *Pycreus*, and other segregate genera (Muasya, 2002).

To varying degrees, the following characteristics undoubtedly contribute to the aggressive, invasive tendencies of *Cyperus* spp. and other sedges: large numbers of small, readily dispersed achenes; vegetative reproduction; longevity of tubers, rhizomes, or other subterranean structures; production of allelopathic compounds; paucity of pathogens; short life reproductive cycle, especially in annual species; tolerance of broad ranges of environmental conditions; C₄ photosynthesis; and resistance to control with herbicides and cultural methods, including tillage.

*Cyperus rotundus* is considered the world’s worst weed because of its ability to survive, spread, and compete, especially in agricultural areas (Holm et al., 1977; Terry, 2001). It was reported in 52 crops and 92 countries (Holm et al., 1977, 1979, 1997). In the U.S.A., Elliott (1821) described *C. rotundus* (C. *hydra* Michx.) as a “scourge” of plantations in Georgia and South Carolina and recommended daily tilling of the soil for control. The infraspecific taxonomy of this cosmopolitan weed is extremely complex and in need of revision (cf. Kükenthal, 1935–1936). In addition to threatening agriculture, *C. rotundus* is a troublesome weed in urban areas and natural communities after disturbance. Although it rarely sets viable seeds (Holm et al., 1977; Thullen & Keeley, 1979), *C. rotundus* produces numerous rhizomes that reportedly can penetrate and grow through fleshy subterranean organs of root crops and even asphalt pavement (Hauser, 1962a, b; Thullen & Keeley, 1979). These rhizomes form tubers that give rise to new aerial plants or produce other rhizomes or they may remain dormant during periods of adverse environmental conditions including heat, cold, drought, flooding, or inadequate aeration (Ranade & Burns, 1925; Williams, 1978; Bendixen & Nandihalli, 1987; Wills, 1987; Miles et al., 1996). The tubers of *C. rotundus* are bitter, rough, and are often connected serially by rhizomes with or without giving rise to new plants (Plowman, 1906; Ranade & Burns, 1925; Hauser, 1962a; Wills & Briscoe, 1970; Holm et al., 1977; Wills, 1987). Dormant tubers make *C. rotundus* difficult to control in turf, and only a few selective herbicides that effectively control sedges are approved for use in turf or in row crops (Aleixo & Valio, 1976; Keeley, 1987; Pereira et al., 1987; Holt & Orcutt, 1996). Tubers and rhizomes of *C. rotundus* produce allelopathic compounds that reduce growth in crops such as cotton (Martinez-Diaz, 1997).

Diagnostic features of *Cyperus rotundus* include abruptly tapering leaves, inflorescence bracts equaling or longer than the inflorescence, and purplish floral scales (Wills & Briscoe, 1970; Horowitz, 1972; Wills, 1987). In a comparative study of *C. rotundus* morphology based on collections from 13 states in the U.S.A. and 21 locations from around the world, Wills (1998) detected differences in numbers of shoots produced by single tubers, numbers of leaves per shoot, lengths and widths of leaves, lengths of culms, flowering times during the year, numbers and lengths of rachises, lengths of rachillae and spikelets, and numbers, lengths, and widths of involucral bracts. Intraspecific variation in *C. rotundus* is also documented in Ceylon (Koyama, 1985), East Africa (Haines & Lye, 1983), and Natal Province (now KwaZulu-Natal Province), South Africa (Gordon-Gray, 1995). Although these differences occurred within some traits on a worldwide basis, the basic characteristics distinguishing *C. rotundus* from other taxa were consistent (Wills, 1998) and differed from closely related taxa such as *C. bifax* C. B. Clarke. Worldwide, *C. rotundus* is a troublesome weed in corn (Zea mays L.), cotton, peanut (*Arachis hypogaea* L.), rice, sorghum (*Sorghum vulgare* Pers.), soybean, sugarcane (*Saccharum officinarum* L.), turf grass species, and many other vegetable, nursery, row, rotation, and plantation crops (Long et al., 1962; Bryson, 1985b; Bendixen & Nandihalli, 1987; Holt & Orcutt, 1991; Derr & Wilcut, 1993; Grichar et al., 1992; Wills, 1998; Bryson et al., 2002, 2003b).

*Cyperus esculentus* is ranked as the world’s 16th worst weed (Holm et al., 1977). Highly variable and widely distributed in tropical, subtropical, and temperate regions around the world, its intraspecific taxonomy was revised by Schippers et al. (1995). Schippers et al. (1993) attribute invasiveness in *C. esculentus* to an increase in the rate of population.
growth brought about by tillage. *Cyperus esculentus* has rhizomes and tubers (Thumbleston & Kommedahl, 1961; Jansen, 1971; Stoller et al., 1972); however, its rhizomes are fleshy and terminate in a sweet-tasting tuber (Garg et al., 1967). Additional diagnostic characters include gradually tapering, acute leaves, yellow to yellowish orange floral scales, and bracts longer than the inflorescence. *Cyperus esculentus* is pernicious and difficult to control in agricultural and urban areas. Although it produces seeds more frequently than *C. rotundus* (Wills, 1987), *C. esculentus* reproduces primarily from tubers (Thumbleston & Kommedahl, 1961). *Cyperus esculentus* tubers remain dormant for prolonged periods during adverse environmental conditions and only produce tubers from rhizomes of the parent plant (Wills, 1987). The tubers of *C. esculentus* are called chufas, tiger nuts, or rush nuts (Abad et al., 2000; DeFelice, 2002). *Cyperus esculentus* is often planted for its tubers that provide food for deer, turkey, wild hogs, and other animals (Miller & Miller, 1999; Abad et al., 2000; DeFelice, 2002). Humans also use the tubers as food for domesticated animals (e.g., chickens, swine) and directly consume them as food, use them as a spice, and use them to prepare a drink called “horchata de chufas” (Zeven & Zhukovsky, 1975; Darby et al., 1977; Allan, 1978; DeFilipps, 1980c; Negbi, 1992; Stephens, 1994; Bryson et al., 1998). Unfortunately, the tubers used by humans contribute to the invasive character of *C. esculentus* and to its dispersal. In addition to the crops mentioned above for *C. rotundus*, *C. esculentus* is also a principal weed of potato (Solanum tuberosum), sugarbeet (Beta vulgaris L.), and many cool-season crops (Bendixen & Nandihalli, 1987).

*Cyperus difformis* and *C. iria* are ranked 32nd and 33rd among the world’s worst weeds, respectively (Holm et al., 1977). Both are caespitose annuals and often produce clumps of many culms and have become established in tropical and temperate areas of the world. In the southeastern U.S.A., *C. difformis* and *C. iria* are primarily weeds of drainage ditches, rice fields, and poorly drained sites in other agricultural fields or disturbed areas. *Cyperus difformis* and *C. iria* produce multiple generations per year under optimal growing conditions and in the tropics flower and produce seeds year-round (Holm et al., 1977). *Cyperus difformis* can complete its life cycle every four to six weeks throughout the growing season (Holm et al., 1977). A single plant of *C. iria* may produce more than 5000 viable seeds, while an individual of *C. difformis* can produce 50,000 seeds with a germination rate of 60% or more (Jacometti, 1912). Short generation times and high seed production favor rapid dispersal (Vaillant, 1967), large seed reservoirs in the soil, high population levels (Holm et al., 1977; Bryson, 1984), and an increased potential for the development of herbicide resistance. In rice-production areas of California, multiple *C. difformis* generations per year and large seed production may be primary factors in the rapid development of herbicide resistance to bensulfuron (Pappas-Fader et al., 1993, 1994; Hill et al., 1994). Despite similarities in habitat and growth and reproductive patterns, *C. difformis* is *C₁* and *C. iria* is *C₂* (Hesla et al., 1982).

*Cyperus rotundus, C. esculentus, C. difformis,* and *C. iria* are all suspected to have originated in Asia. Other *Cyperus* spp. of probable Asian origin include *C. compressus, C. haspan, C. pilosus,* and *C. sanguinolentus* (Holm et al., 1979). All are naturalized weeds in other regions of the world (Bryson & Carter, 1995; Carter & Bryson, 2000b).

*Cyperus haspan* is among the world’s worst weeds (Holm et al., 1997). It has been reported as a weed in 12 crops and 39 countries throughout tropical and semitropical areas of Africa, Asia, Australia, South America, and North America (Lin, 1968; Holm et al., 1977, 1979; Kissmann, 1997). *Cyperus haspan* is a recent introduction into Hawaii with the first collection made in 1957 (Wagner et al., 1990). An individual plant can produce more than 50,000 achenes per year (Datta & Banerjee, 1976), and although plants produce achenes during the first season of growth, they do not form rhizomes until the second year (Tadulingam & Venkatanaryana, 1955). *Cyperus haspan*, a *C₁* plant, commonly occurs in shallow standing water and germinates and grows well in wet, sandy, acidic soils (Bertels, 1957; Eyles & Robertson, 1963; Dirven, 1970). *Cyperus haspan* is sometimes broken into two subspecies: *C. haspan* subsp. *juncoideus* (Lam.) Kük. is a taller plant with conspicuous rhizomes (Kükenthal, 1935–1936; Kern, 1974; Koyama, 1985). *Cyperus haspan* is sometimes confused with closely related *C. tenuispi-
ca Steud., a species with more widely spaced floral scales, and both species are cited as frequent weeds in rice fields in Asia (Kern, 1974; Koyama, 1985).

*Cyperus enterianus* is native to temperate regions of South America; it is also known from the Caribbean, Mexico, and the Coastal Plain of the southern U.S.A. (Kükenthal, 1935–1936; Barros, 1960; Carter, 1990; Tucker, 1994). In his comprehensive revision of *Cyperus*, Kükenthal (1935–1936) accorded specific rank to *C. enterianus*; however, Barros (1960) reduced it to varietal status under *C. luzulae* (L.) Rottb. ex Retz., and Denton (1978) gave it no rank, treating it as a synonym of *C. luzulae*. Carter (1990) and subsequent authors (Tucker, 1994; Tucker et al., 2002) treated this taxon at the rank of species. In the southeastern U.S.A., flooding, construction equipment, mowing, and soil-moving activities, especially along highways, disperse the small achenes of *C. enterianus*, resulting in infestations in a variety of disturbed habitats (Carter, 1990; Carter & Bryson, 1996). *Cyperus enterianus* displaces native vegetation even in undisturbed habitats, and, without widespread control, it will likely continue to spread rapidly, infesting agricultural, forested, riparian, and urban areas. Figure 4 shows the dispersal of *C. enterianus* in the U.S.A., where by 2003 it was documented in 43 counties from Florida and southern Georgia into southeastern Texas. In the southern U.S.A., *C. enterianus* reproduces copiously from achenes and spreads vegetatively and perennates from short rhizomes. *Cyperus enterianus* is a prolific seed producer, with the number of seeds per inflorescence ranging from 1000–20,000+ depending on the size and maturity of plants and mature plants (> 1 year old) producing 10–100+ inflorescences per year (Carter & Bryson, 1996; Bryson et al., 2003a). Preliminary seed germination studies indicate moderate to high viability (55%–95%) (Carter & Bryson, 1996). In the southeastern U.S.A., *C. enterianus* flowers and fruits from June until frost in November or December (Carter, 1990; Carter & Jones, 1991; Bryson & Carter, 1994). *Cyperus enterianus* continues to spread at an alarming rate and threatens agricultural and natural areas. Also, preliminary studies suggest that populations will potentially spread northward into Arkansas, North Carolina, South Carolina, Tennessee, and Virginia. Additional research is needed to determine more effective methods of prevention and control.

*Cyperus acuminatus* Torr. & Hook., *C. eragrostis*, *C. luzulae*, *C. ochraceus*, *C. pseudovegetus*, *C. reflexus*, *C. surinamensis*, and *C. virens* are cited as weeds (Appendix 2) and are classified with *C. enterianus* in *Cyperus* sect. Luzuloidei Kunth (Kükenthal, 1935–1936; Denton, 1978). *Cyperus acuminatus*, *C. pseudovegetus*, and *C. virens* are all native to North America, where they are currently relatively minor weeds; however, they could become problems if introduced beyond their native ranges. *Cyperus pseudovegetus* is widely distributed in eastern North America (Denton, 1978; Tucker et al., 2002). In the U.S.A., *C. pseudovegetus* and *C. virens* are common in disturbed, intermittently wet soils, e.g., roadside ditches, margins of ponds, and swales in fields, pastures, and grasslands. *Cyperus virens* is widely distributed in the New World, ranging from South America, Central America, the Caribbean Islands, Mexico, and the southern U.S.A. (Denton, 1978), and is recently introduced into Hawaii with the first collection made in 1976 (Wagner et al., 1990). Several infraspecific taxa have been recognized (Denton, 1978), including *C. virens* var. *drummondii*. Carter et al. (1999) showed that *C. drummondii* is specifically distinct from *C. virens* and in the southeastern U.S.A. has a more restricted distribution and habitat and is less weedy than *C. virens*. *Cyperus reflexus* occurs in temperate South America, Central America, Mexico, and in the U.S.A. (Denton, 1978; Tucker, 1994). It is introduced in Australia, where it is naturalized near Sydney (Wilson, 1993). In the U.S.A., *C. reflexus* is most common in southeastern Texas and Louisiana, where it is found in intermittently wet, disturbed soils of ditches, fields, and grasslands (Denton, 1978; Carter, pers. obs.); it has also been reported in western Florida (Wunderlin, 1998). Additional research is needed to elucidate the relationship between *C. fraternus* Kunth and *C. reflexus*, which has been treated as *C. reflexus* var. *fraternus* (Kunth) Kuntze (Kükenthal, 1935–1936; Denton, 1978). *Cyperus ochraceus* is widespread in the New World and is known from South America, Central America, Mexico, the U.S.A., and the Caribbean Islands (Denton, 1978). It is currently only a minor weed in the southern U.S.A., where it is found in disturbed, intermittently wet soils and is most common in Texas and Louisiana but has dispersed to scattered sites elsewhere (Denton, 1978; Tucker et al., 2002; Carter, pers. obs.).
Cyperus surinamensis is widely distributed in the New World, ranging from South America, Central America, Mexico, and the Caribbean Islands into southeastern and south-central U.S.A. (Denton, 1978). Readily identified by its retrorsely scabrid culms, C. surinamensis has been cited as a weed in both North and South America (WSSA, 1989; Kissman, 1997). In warmer parts of the southeastern U.S.A., it is a common weed in a variety of open disturbed sites with hydric soils.

Cyperus eragrostis occurs naturally in South America and in California, Oregon, Washington, and British Columbia in North America (Denton, 1978). It has been used ornamentally, which in part accounts for its introduction into other parts of the world (Tucker, 1987; Sell & Murrell, 1996; Darke, 1999; Petřík, 2003). It occurs sporadically in the eastern U.S.A., where it is introduced and appears to be spreading (Bryson & Carter, 1994; Bryson et al., 1996; Tucker et al., 2002). Cyperus eragrostis is naturalized in Australia and has expanded its range and frequency there, where it is a weed of rice and ephemeral wet, disturbed sites (Wilson, 1993). In reporting C. eragrostis new to the Czech Republic, Petřík (2003) provides a thorough account of its invasion of Europe, where it is widely distributed and has been known since the mid-1800s. Given its association with rice as a weed in Australia, C. eragrostis could become a problem in rice agriculture in the southeastern U.S.A. and elsewhere. Additional research is needed to determine more about the distribution and dispersal of C. eragrostis, its potential to become an agricultural pest, and its control.

Cyperus oxylepis Nees ex Steud. and C. elegans L. are widely distributed in tropical, subtropical, and warm temperate regions of the New World. Both species have viscid foliage and are markedly aromatic, with the fragrance of cedar wood (Juniperus virginiana L.) sometimes sensed in the field before the plants are seen. The floral scales of C. oxylepis are golden brown and those of C. elegans are greenish tan. Cyperus oxylepis, listed as a weed (WSSA, 1989), is apparently expanding its range in coastal areas of the southeastern U.S.A. (O’Neill, 1938b; Thieret, 1964; Tucker, 1987; Bryson & Carter, 1992; Bryson et al., 1996), where it is found in disturbed clay soils of salt marshes.

A number of aquatic Cyperus species cultivated in ponds and water gardens have become naturalized. All have the potential to become invasive weeds in aquatic and wetland habitats in tropical and subtropical areas, and at least one, C. prolifer, is invasive in the U.S.A. (Carter et al., 1996). Trade and importation of these species should be carefully regulated to prevent further impact. Cyperus alternifolius subsp. flabelligeriformis has been used as an ornamental in water gardens and as a potted plant for more than 200 years (Bailey & Bailey, 1976) and is widely naturalized from cultivation in the tropics and subtropics and other warm areas (Bailey, 1935, 1949; O’Neill, 1946; Kern, 1974; DeFilipps, 1980c; Koyama, 1985; Wagner et al., 1990; Sell & Murrell, 1996). It has been variously known as C. alternifolius subsp. flabelligeriformis Kük.; C. flabelligeriformis Rottb., nom. illeg.; and C. involucratus Rottb. In the U.S.A. it is naturalized in Florida, Louisiana, Texas, and California, where it is occasionally found in moist to hydric soils of roadside ditches, stream banks, vacant lots, and other disturbed sites (Carter, pers. obs.; Tucker et al., 2002). In his worldwide monograph of Cyperus, Küchenthal (1935–1936) recognized two subspecies: C. alternifolius subsp. alternifolius and C. alternifolius subsp. flabelligeriformis. Baijnath (1975) treated these as species and stated that C. alternifolius is rare and mostly restricted to Madagascar where it is native and that C. involucratus [= C. alternifolius subsp. flabelligeriformis] is the correct name for the widely naturalized cultivated plant indigenous to Africa. More recently, Gordon-Gray (1995) adopted Küchenthal’s taxonomy, indicating the need for additional critical investigation of this complex in southern Africa, which also includes the related cultivated aquatics C. sexangularis and C. textilis. Until further research elucidates the relationships among these taxa, we have adopted the more conservative taxonomy of Küchenthal (1935–1936) and Gordon-Gray (1995), recognizing two subspecies within C. alternifolius. Although popular in water gardens in southern Africa, C. sexangularis survives under drier conditions in the absence of extended water stress (Gordon-Gray, 1995), and C. textilis is naturalized in the Azores (DeFilipps, 1980c). Thus, it would appear that C. alternifolius, C. sexangularis, and C. textilis have the potential to become invasive pests in a variety of aquatic, wetland, and terrestrial habitats in tropical and subtropical regions.

Cyperus prolifer is sold as an ornamental for water gardens (Bailey & Bailey, 1976; Simpson, 1994) and has been variously listed as Cyperus has-
C. papyrus is classified cv. ‘nanus’ (Bailey & Bailey, 1976); however, forms dense stands in aquatic and wetland habitats and dominates swamps with low biodiversity in northern Uganda (Mabberley, 1997). Plants may grow to 5 m high, making it one of the largest sedges (Koyama, 1985), and it is cultivated as an ornamental and curiosity in greenhouses and outdoors in ponds and water gardens in tropical and subtropical regions of the world (Bailey, 1935, 1949; Bailey & Bailey, 1976). *Cyperus papyrus* is naturalized in Florida, U.S.A. (Kükenthal, 1935–1936; Koyama, 1985; Carter et al., 1996). It is a robust plant to 1.5 m high and in its habit and general inflorescence pattern resembles the tropical species *C. imbricatus* Retz. Both taxa were placed in section *Exaltati* Benth. by Kükenthal (1935–1936). Its size in combination with other characters make *C. imbricatus* a striking plant in the field: broad bracts and leaf blades (to 15 mm wide) with contrasting surfaces (adaxial light green, abaxial glaucous), and a branched inflorescence with spikes of densely clustered golden-brown spikelets (Carter et al., 1996).

Although it seems to be more clearly allied with subgenus *Cyperus* (Kükenthal, 1935–1936; Koyama, 1985), it has characteristics that seem to defy placement there: namely, a bicarpellate gynoecium with two stigmas and a lenticular achene with face adjacent to rachilla. When taken alone, the gynoecium and fruit characteristics seem to indicate a relationship with subgenus *Cyperus* (Kükenthal, 1935–1936; Koyama, 1985), which supports inclusion in subgenus *Cyperus*. In central Florida, where this emergent aquatic sedge was probably introduced with nursery stock used to revegetate a reclamation wetland in an abandoned phosphate pit, *C. alopecuroides* exhibits invasive characteristics, forming extensive stands in shallow water and floating mats (Carter et al., 1996).

According to Kantor (1999), *C. alopecuroides* was cultivated by the ancient Egyptians and its inflorescence was widely depicted in one of the characteristic motifs of their decorative art. Additional research on *C. alopecuroides* is needed to understand better its potential for becoming an invasive weed and its phylogenetic relationships.

*Cyperus odoratus* is widely distributed in tropical and subtropical regions around the world (Kükenthal, 1935–1936; Kern, 1974) and is generally found in disturbed hydric soils and wetlands. It is frequently cited as a weed and has been listed as a pest of rice (Appendix 2). In the southeastern U.S.A., *C. odoratus* is commonly found in wet disturbed sites, e.g., ditches, stream banks, swamps, wetlands, and edges of ponds, but it is not of major economic importance. *Cyperus odoratus* is classified in subgenus *Diclidium* (Schrad. ex Nees) C. B. Clarke [= *Torulinium*] characterized by spikelets that disarticulate into one-fruited segments (Kükenthal,
1935–1936), and its achenes, enclasped within corky rachilla segments, are dispersed by water (Kern, 1974; Haines & Lye, 1983). Jones et al. (1996) recognized several infraspecific taxa of this variable species in North America. In the U.S.A., *C. odoratus* is frequently associated with *C. erythrorhizos* Muhl., which is also listed as a weed (Holm et al., 1979; WSSA, 1989). *Cyperus erythrorhizos*, a widespread annual sedge restricted to North America (Kükenthal, 1935–1936; Tucker et al., 2002), inhabits disturbed hydric soils of wetlands, ditches, stream banks, floodplains, edges of ponds and swamps, swales in fields and pastures, and occasionally rice fields. It is of minor economic importance. *Cyperus digitatus* Roxb. is closely related to *C. erythrorhizos*, but it is perennial and generally a much larger plant. *Cyperus digitatus* is widely distributed in tropical and subtropical regions of both the Eastern and Western hemispheres (Kükenthal, 1935–1936; Kern, 1974; Koyama, 1985) and, as can be seen in Appendix 2, is frequently cited as a weed. Because it is much more wide-ranging and cited as a pest of rice in the Eastern Hemisphere (Kern, 1974), *C. digitatus* is probably of greater economic significance than *C. erythrorhizos*.

*Cyperus articulatus* L. ranges widely in tropical, subtropical, and warm temperate regions around the world (Kükenthal, 1935–1936). It is a rhizomatous perennial with a reed-like habit, septate culms, and bladeless (usually) leaves. In the southeastern U.S.A., *C. articulatus* occurs near the coast in marshes, ditches, or other open disturbed sites, and populations usually appear as scattered, solitary aerial stems. As shown in Appendix 2, *C. articulatus* is widely reported as a weed (Holm et al., 1979; Kühn, 1982; WSSA, 1989; Kissman, 1997).

*Cyperus compressus* is widely distributed in tropical, subtropical, and warm temperate regions around the world (Kükenthal, 1935–1936). It is frequently cited as a weed and is found in a variety of habitats disturbed and altered by humans, e.g., waste places, grasslands, lawns, crops, roadsides, fallow rice fields (Ohwi, 1965; Lin, 1968; Kern, 1974; Kühn, 1982; Koyama, 1985; WSSA, 1989; Ravi & Mohanan, 2002). In warmer parts of the southeastern U.S.A., it is a common weed in sandy loam soils of agricultural fields, roadsides, gardens, and other disturbed sites. According to Bailey (1935) and Huxley (1992), *C. compressus* has been cultivated as an ornamental, which probably partly accounts for its wide distribution.

*Cyperus pilosus* is a weed of tropical, subtropical, and warm temperate areas in Asia, western Africa, and Australia (Kükenthal, 1935–1936; Koyama, 1985; Wilson, 1993) and is commonly cited as a weed of rice (McGivney, 1938; Kern, 1974; Wagner et al., 1990). It has been collected in Hawaii, where it was possibly introduced with rice agriculture, but has not been found there since 1916 (Wagner et al., 1990). *Cyperus pilosus* has been known in the southeastern U.S.A. since 1938, where it was probably introduced through the cultivation of rice (McGivney, 1938; O’Neill, 1938a). In the southeastern U.S.A., it is found in rice fields, wet ditches, and other wet disturbed sites and is apparently spreading, having been reported new to several states in recent years (Burkhalter, 1985; Bryson & Carter, 1992; Tucker et al., 2002). *Cyperus procerus* Rottb. is related to *C. pilosus*. It is known from tropical and subtropical regions of western Africa, India, Asia, Malaysia, and Australia (Koyama, 1985; Wilson, 1993) and has been cited as a weed of rice fields in Asia and western Africa (Hooper & Napper, 1972; Kern, 1974). *Cyperus pilosus* and *C. procerus* share several characteristics that distinguish them from most other *Cyperus* spp.: stoloniferous habit, triquetrous culm, and hispidulous rachis.

*Cyperus sphacelatus* Rottb. is widely distributed in the tropics and subtropics from eastern Africa, Ceylon, Malaysia, northern Australia (Queensland), Tahiti, South America, Central America, and the Caribbean (Clarke, 1900; Uittien, 1932; Kükenthal, 1935–1936; Haines & Lye, 1983; Tucker, 1983; Koyama, 1985). It is a heliophyte of moist disturbed sites, beaches, riverbanks, fields, and roadsides (Reed, 1977; Tucker, 1983; Carter et al., 1996), and, in Malaysia, *C. sphacelatus* is reported as a common weed on airstrips (Kern, 1974), which suggests dispersal via air traffic. Mohr (1901) reported *C. sphacelatus* from ballast heaps in Mobile, Alabama, U.S.A., and more recently naturalized populations have been found in southern Florida, U.S.A. (Carter et al., 1996). An analysis of floral scale length on herbarium specimens indicates that the populations in Florida probably originated from the West Indies (Carter et al., 1996). The recent discovery of naturalized populations in peninsular Florida suggests that *C. sphacelatus* is currently
undergoing range expansion in the southeastern U.S.A. Field botanists and weed scientists should be vigilant to detect additional populations of this introduced pest, and appropriate governmental agencies should initiate measures to survey for and eradicate populations of *C. sphaelatus* in the U.S.A. before it spreads further. The following combination of characteristics distinguishes *C. sphaelatus* from other *Cyperus* spp.: annual caespitose habit, triquetrous achene, diffuse inflorescence with flattened spikelets, and variegated floral scales pale, nearly white, each with two conspicuous reddish patches.

*Cyperus distans* L. f. is a pantropical weed of marshes, in Africa, India, Sri Lanka, southeastern Asia, Malaysia, southern China, the Philippines, the Caribbean islands, Central America, Mexico, and tropical South America (Clarke, 1900; Uittien, 1932; Kükenthal, 1935–1936; Koyama, 1985; Adams, 1994; Tucker, 1994). *Cyperus distans* is frequently cited as a weed in the Eastern Hemisphere, where aquatic biotypes are known, and it is a pest of rice fields and grasslands (Appendix 2). It occurs sporadically in the southeastern U.S.A. and has been reported from coastal North Carolina, Georgia, and Florida (Small, 1933; Kükenthal, 1935–1936; McGivney, 1938; Radford et al., 1968; Beal, 1977; Carter et al., 1996). The recent report (Carter et al., 1996) from Florida, U.S.A., suggests that *C. distans* is expanding its range there. The following combination of characteristics distinguishes *C. distans* from other *Cyperus* spp.: rhizomes; scales ascending, remote, with 3- to 5-nerved greenish keels, sanguineous to reddish brown nerveless sides, and with scarious emarginate tips. Field botanists and weed scientists should seek and report additional populations, and appropriate state and federal agencies should undertake eradication measures to ensure early control of this potentially invasive pest in the southeastern U.S.A.

A number of species classified by Kükenthal (1935–1936) in *Cyperus* sect. *Umbellati* C. B. Clarke are listed as weeds in Appendix 2. *Cyperus cyperinus* (Retz.) Suringar and *C. cyperoides* (L.) Kuntze are broadly distributed in warm parts of the Eastern Hemisphere (Kükenthal, 1935–1936; Kern, 1974). *Cyperus cyperoides* is introduced in the West Indies (Kükenthal, 1935–1936; Kern, 1974), and *C. cyperinus* has been reported as a wool alien in Great Britain (Sell & Murrell, 1996). Both species have frequently been cited as weeds (Appendix 2). The variation within these species is complex and poorly understood, with numerous infraspecific taxa recognized, and the synonymy is formidable (cf. Kükenthal, 1935–1936; Kern, 1974; Haines & Lye, 1983; Koyama, 1985). No thorough systematic review of this group has been done since Kükenthal (1935–1936). Additional research to elucidate the relationships of infraspecific taxa and their relationships with one another and with related species, e.g., *C. panicus* Boeckeler, is needed. Such research with North American species of section *Umbellati* has been productive, resulting in substantial taxonomic and nomenclatural clarification (Carter, 1984; Carter & Jarvis, 1986; Carter & Kral, 1990; Carter & Jones, 1997).

*Cyperus croceus* Vahl, *C. echinatus* (L.) A. W. Wood, and *C. retrorsus* Chapm. are listed as weeds by WSSA (1989). All are caespitose perennials with umbelliform inflorescences of simple spikes of densely clustered spikelets, classified by Kükenthal (1935–1936) in section *Umbellati*. These taxa are native and widely distributed in the southeastern U.S.A., where they are found in lawns, pastures, roadsides, waste places, disturbed woodlands, and other ruderal sites (Carter, 1984). *Cyperus croceus* and *C. echinatus* were long known as *C. globulosus* auct. non Aubl. and *C. ovularis* (Michx.) Torr., respectively (Carter & Kral, 1990). *Cyperus croceus* also occurs in the Caribbean Islands (Carter, 1984). *Cyperus croceus* and *C. echinatus* have been reported as wool aliens in Great Britain (Sell & Murrell, 1996), and *C. croceus* has been associated with bal-last (Britton, 1886). *Cyperus echinatus* is reportedly naturalized in the Azores (DeFilipps, 1980c). Carter (1984, in prep.) shows that plants with ascending yellowish scales are distinct from *C. retrorsus* and should be called *C. ovatus* Baldwin. *Cyperus ovatus* is a coastal species in the southeastern U.S.A., which is found in slightly wetter sites than related *C. retror-sus*, e.g., moist ditches, disturbed sites in moist sandy, loamy, or peaty soils in coastal flatwoods (Carter, 1984, in prep.). Although not listed by WSSA (1989), we include the related taxa *C. retroflexus* Buckley and *C. floribundus* (Kük.) R. Carter & S. D. Jones in Appendix 2, because they are commonly weeds of roadsides, poorly kept lawns, pastures, disturbed grasslands, and agricultural...
fields; see Carter and Jones (1997) for clarification of the taxonomy of *C. retroflexus* and its allies. *Cyperus floribundus* is native to northeastern Mexico and southern Texas (Carter, in prep.). *Cyperus retroflexus* ranges from northern Mexico north through Texas into Oklahoma and east into western Mississippi, Arkansas, and Missouri and is apparently expanding its range eastward into Alabama, Mississippi, and Missouri (Carter et al., 1987; Carter & Bryson, 1991a, b). *Cyperus pluknetii* also belongs to section *Umbellati*. It has spikelet modifications facilitating animal dispersal (Carter, 1993) and is endemic to the eastern U.S.A., where it is well adapted to open xeric sands of the Coastal Plain (Carter, 1984, in prep.). *Cyperus pluknetii* currently does not appear to be invasive in its natural range; however, because of its specialized dispersal mechanism and adaptation to dry soils, it could potentially become an invasive weed if introduced into suitable habitat elsewhere.

*Cyperus aggregatus* is frequently cited as a weed (Appendix 2) and has been classified in section *Umbellati* (Kükenthal, 1935–1936). The species was previously called *C. flavus* (Vahl) Nees, nom. illeg., non J. Presl & C. Presl and *C. cayennensis* (Lam.) Britton, non. illeg., non Willd. ex Link (Tucker, 1985). *Cyperus aggregatus* is native to Central and South America, was introduced with ballast in the U.S.A. (Britton, 1886; Mohr, 1901; Horvat, 1941; Tucker et al., 2002), and is also introduced and weedy in Australia (Wilson, 1993). *Cyperus aggregatus* occurs sporadically in the Coastal Plain of the southeastern U.S.A., where it can be locally abundant and somewhat invasive on open, disturbed sandy soils (Bryson & Carter, 1992; Tucker et al., 2002; Carter, pers. obs.). It is likely to continue to expand its range in warmer parts of the southeastern U.S.A. and elsewhere.

*Cyperus ligularis* L. is occasionally cited as a weed (Appendix 2). It is widely distributed in the West Indies, Mexico, Central America, and South America and is introduced in Africa and the southeastern U.S.A. (O’Neill, 1946; Tucker et al., 2002). It is a frequent weed of disturbed sites in southern peninsular Florida, U.S.A. (Wunderlin, 1998), and Mohr (1901) reported that it was collected in 1891 on ballast at Mobile, Alabama, U.S.A., where it has apparently not survived. Thus, *C. ligularis* is apparently not tolerant of prolonged cold temperatures. *Cyperus ligularis* is readily identified by its robust caespitose habit; coarse lacerating leaves; grayish green foliage; umbelliform inflorescence of dense, oblong-cylindric, often branched spikes; and reddish brown floral scales.

A number of *Cyperus* species colonize coastal or inland sand dunes by forming extensive rhizomes. *Cyperus dentatus* Torr., *C. lecontei* Torr. ex Steud., and *C. onerosus* M. C. Johnst. are related North American species sharing similar growth forms and habitats, spreading vegetatively through growth of rhizomes. *Cyperus lecontei* is listed as a weed by the WSSA (1989), and we have observed it colonizing disturbed sandy roadides and other open sandy areas along the Gulf Coast. *Cyperus lecontei* and *C. dentatus* are coastal fringe species. *Cyperus lecontei* is found on exposed sands of coastal dunes and swales in the southeastern U.S.A., and *C. dentatus* occupies similar habitats but with a more northerly distribution from the mid-Atlantic states north into the maritime provinces of Canada (Tucker et al., 2002). *Cyperus onerosus* is a related species endemic to swales and pools far inland in nonmaritime dune formations in western Texas (Carter, pers. obs.; Tucker et al., 2002). Rhizomes of *C. dentatus* form tubers, but do not in *C. lecontei* and *C. onerosus* (Tucker et al., 2002). *Cyperus arenarius* Retz. ranges from southern Iran through Pakistan, India, and Ceylon into Indochina (Kükenthal, 1935–1936; Koyama, 1985) and has been introduced into southern Australia and southern Africa (Kukkonen, 2001). Simpson and Inglis (2001) listed it as a weed, and Koyama (1985: 209) described it as a coastal species in Ceylon commenting that its “extensive rhizome system … forms a large pure community.” The endemic *C. crassipes* Vahl from coastal southeastern Africa has a similar habit and habitat: sandy seashores and riverbanks (Gordon-Gray, 1995). *Cyperus stoloniferus* Retz., another vegetative colonizer of coastal sands, ranges from Pakistan and India to China and northern Australia and is also known from Mauritius and Madagascar (Kukkonen, 2001). Although only *C. arenarius* and *C. lecontei* are listed in Appendix 2, we think these ecologically similar species have great potential to invade coastal dunes or other open sandy areas, if introduced outside their natural ranges, as the alien *Carex kobomugi* has done along the mid-Atlantic coast of North America (Standley, 1983).
Cyperus fuscus is native to Eurasia and the Mediterranean region of northern Africa and has spread in Asia and Africa and into Greenland, Iceland (Kükenthal, 1935–1936; DeFilipps, 1980c), and North America (Smith, 1867; Britton, 1886; Knowlton et al., 1911; McGivney, 1938; McKenzie et al., 1998). This small caespitose annual produces large numbers of tiny achenes. It is reported as a weed in rice-producing areas of Asia and Portugal and is a common weed in Afghanistan and Israel (Weedon & Stephens, 1969; Holm et al., 1977; Zhirong et al., 1990). Early records of *C. fuscus* in North America were mostly associated with ballast waste and wharf areas (Britton, 1886; Rhoads & Klein, 1993). *Cyperus fuscus* seems to be expanding its range in the U.S.A. (McKenzie et al., 1998), where it is possibly still in the lag phase and could pose problems in the future for rice agriculture.

*Cyperus amabilis* Vahl, *C. cuspidatus* Kunth, and *C. squarrosus* L. are widely distributed in tropical, subtropical, and warm temperate regions of both the Eastern and Western hemispheres (Kükenthal, 1935–1936; Kern, 1974). All three are diminutive sedges listed in Appendix 2, and both *C. amabilis* and *C. cuspidatus* have prominently cuspidate floral scales. *Cyperus amabilis* has been reported as a weed (Healy & Edgar, 1980; Kühn, 1982) and is known from Africa, Asia, South America, Central America, and North America (Kükenthal, 1935–1936; Tucker et al., 2002). As shown in Appendix 2, *C. cuspidatus* and *C. squarrosus* are listed as weeds of rice and are also found in waste places, disturbed sites, sandy fields, and grasslands. In warmer parts of the southeastern U.S.A., *C. cuspidatus* is sometimes locally abundant in disturbed sandy soils in and around agricultural fields and has also been observed as a weed in container-grown plants and plant nurseries (Carter, pers. obs.). *Cyperus squarrosus* is characterized by the distinctive aroma of fenugreek (*Trigonella foenum-græcum* L.), which is shared by *C. fuscus*, *C. hyalinus* Vahl, and *C. setigerus* Torr. & Hook. (McKenzie et al., 1998; Carter & Mears, 2000). Kern (1974) showed that *C. aristatus* Rottb. is a synonym of *C. squarrosus*, and, subsequently, contemporary workers have followed Kern without reviewing the status of a number of varieties and forms of *C. aristatus* recognized by Kükenthal (1935–1936). North American plants have been segregated as *C. inflexus* Muhl. or *C. aristatus var. inflexus* (Muhl.) Boeckeler. Preliminary research (Carter, unpubl. data) indicates that *C. inflexus* is a smaller plant with smaller spikelets and scales and supports its recognition as a distinct endemic North American taxon. The names *C. inflexus* and *C. squarrosus var. runyonii* (O’Neill) S. D. Jones & Wipff were placed into synonymy, without justification, under *C. squarrosus* by Tucker et al. (2002). *Cyperus granitophilus* McVaugh is an autotetraploid derivative of *C. squarrosus*, endemic to granite and sandstone outcrops in the Piedmont region from Virginia to Georgia, U.S.A. (Garoni & Murdy, 1964; Tucker et al., 2002). Preliminary observations (Carter, unpubl. data) indicate that *C. granitophilus* is a coarser plant than the more common widespread *C. inflexus* and is morphologically more similar to *C. squarrosus*. Although new taxa have been described and other major nomenclatural changes have occurred, the entire complex has not been studied since Kükenthal (1935–1936). A systematic review worldwide of *C. squarrosus* and related taxa is needed to achieve a consistent treatment of these and other infraspecific taxa not accounted for by contemporary authors.

*Cyperus gracilis* R. Br., yet another diminutive sedge cited as a weed (Holm et al., 1979), is native to Australia, where it grows in open woodlands and grasslands in drier sites than related species (Wilson, 1993). It was once promoted for use as a ground cover in Hawaii, where it is naturalized and common in disturbed sites, lawns, and roadsides (Hughes, 1995). It is also introduced in California, U.S.A. (Tucker et al., 2002).


*Cyperus sanguinolentus* has been frequently cited as a weed (Holm et al., 1977; Reed, 1977; Kühn, 1982; Zhirong et al., 1990). It is widely distributed in the Eastern Hemisphere, where it is known from northeastern Africa, the Middle East,
India, Sri Lanka, central Asia, southeastern Asia, China, Taiwan, Japan, Korea, the Philippines, Indonesia, Malaysia, and Australia (Clarke, 1894; Kükenth, 1935–1936; Ohwi, 1965; Kern, 1974; Holm et al., 1977; Reed, 1977; Kühn, 1982; Haines & Lye, 1983; Zhirong et al., 1990; Wilson, 1993). In the Western Hemisphere, it has been reported from Hawaii (Wagner et al., 1990) and from the Coastal Plain of the southeastern U.S.A. in North America (Carter & Bryson, 2000b, 2001). *Cyperus sanguinolentus* is a weed in paddy and damp, low-dryland crop fields in Asia (Holm et al., 1977; Zhirong et al., 1990). In the southeastern U.S.A. it is a locally common annual weed in periodically disturbed sites with hydric soils, e.g., road ditches and margins of artificial ponds (Carter & Bryson, 2000b). Its introduction into the southeastern U.S.A. is associated with the cultivation of rice, and its dispersal and range expansion there are associated with road construction and maintenance activities (Carter & Bryson, 2000b). *Cyperus louisianensis* Thieret, once thought to be a rare endemic species in southern Louisiana, U.S.A. (Thieret, 1977), has been shown to be the nonindigenous weed *C. sanguinolentus* (Carter & Bryson, 2000b).

*Cyperus flavescens* is widely distributed in both Old and New Worlds (Kükenthal, 1935–1936; O’Neill, 1946; Barros, 1960; Haines & Lye, 1983; Tucker et al., 2002). It is a common weed of seeps, roadside ditches, and disturbed wet sites in Natal Province (now KwaZulu-Natal Province), South Africa (Gordon-Gray, 1995). In the U.S.A. it is a common tuft-forming weed in drainage ditches, disturbed hydric sites, and moist lawns and fields (Carter, pers. obs.), ranging widely from Florida north into southern Canada and west to Texas and Missouri (Tucker et al., 2002). *Cyperus lanceolatus* is similar to *C. flavescens* and frequently occurs in the same habitats in the southeastern U.S.A. Both taxa have similar habits (dense tufts) and differ primarily in the color of their achenes: black in *C. flavescens*, brown in *C. lanceolatus*. Apparently less tolerant of cold winter temperatures, *C. lanceolatus* is restricted to the warmest parts of the southeastern U.S.A., ranging from Florida north into southern Georgia then west along the coast to Texas (Bryson et al., 1996; Tucker et al., 2002). *Cyperus lanceolatus* also occurs in the West Indies, Mexico, Central and South America, and Africa (O’Neill, 1946; Barros, 1960; Haines & Lye, 1983; Tucker, 1994). Although the type locality is Georgia, U.S.A. (Elliott, 1821), *C. fasciculatus* Elliott is not cited by contemporary American authors (e.g., Tucker, 1994; Tucker et al., 2002) but is cited as a weed in Asia (Appendix 2). This problem should be researched to determine how the name *C. fasciculatus* impinges on nomenclature of the North American plants currently known as *C. flavescens* and *C. lanceolatus*.

*Cyperus polystachyos* is a cosmopolitan weed, widely distributed in tropical, subtropical, and warm temperate areas (Uittien, 1932; Kükenthal, 1935–1936; Barros, 1960; Kern, 1974; DeFilipps, 1980e; Haines & Lye, 1983; Tucker, 1983, 1994; Koyama, 1985; Wilson, 1993; Adams, 1994; Gordon-Gray, 1995). *Cyperus polystachyos* is cited as a weed of hydric soils in ditches, waste places, grasslands, and disturbed agricultural areas and fields, including rice fields (Kern, 1974; Haines & Lye, 1983). *Cyperus polystachyos* is taxonomically and nomenclaturally complex. Kükenthal (1935–1936) segregated 16 infraspecific taxa from *C. polystachyos* (11 varieties, 5 forms). Also, the relationships between *C. polystachyos* and related taxa like the North American species *C. filicinus* Vahl and *C. fuga* Liebm. are poorly understood and are in need of clarification. We have observed at least three entities passing as *C. polystachyos* in the southeastern U.S.A., with the greatest diversity centered along the Gulf Coast. This group is in need of critical taxonomic review on a worldwide basis. *Cyperus polystachyos* is cited as a weed of hydric soils in ditches, waste places, grasslands, and disturbed agricultural areas and fields, including rice fields (Kern, 1974; Haines & Lye, 1983).

*Cyperus flavicomus* is found in North America, South America, and Africa (Kükenthal, 1935–1936; Barros, 1960; Tucker, 1994) and in Appendix 2 is cited as a weed of waste places, rice fields and various other crops, pastures, and turf. *Cyperus flavicomus* occurs sporadically on moist soil in and around agricultural fields in the southeastern U.S.A., where it is of minor importance as a weed. *Cyperus pumilus* is a diminutive, densely tufted annual and a minor weed of disturbed sandy soils of rice fields and fallow fields (Kern, 1974; Haines & Lye, 1983; Carter, pers. obs.). As shown in Appendix 2 it is widespread in the Old World. In the New World, *C. pumilus* is known from the West Indies and the U.S.A.
(Kükenthal, 1935–1936; Kern, 1974; Haines & Lye, 1983; Koyama, 1985; Gordon-Gray, 1995). In the U.S.A., *C. pumilus* has long been known from Florida (Chapman, 1889 [as *C. divergens* Kunth]; Small, 1933; Long & Lakela, 1971; Godfrey & Wooten, 1979; Clewell, 1985; Wunderlin, 1998) and was reported in 1996 in southern Georgia (Bryson et al., 1996). *Cyperus pumilus* appears to be spreading in the southeastern U.S.A., as plants were found in northern Georgia in 2003 (M. Czarnota s.n., 29 January 2003, VSC).

*Cyperus hyalinus* is transitional between *Cyperus* and *Kyllinga* and is pragmatically treated here in subgenus *Queenslandiella* (Domin) Govind. Its taxonomic affinities are unclear, and it has been variously placed in *Pycreus*, *Kyllinga*, *Cyperus*, and the monotypic genus *Queenslandiella* based on morphological traits (Clarke, 1884; Kükenthal, 1935–1936; Kern, 1974; Govindarajalu, 1975; Haines & Lye, 1983). However, recent molecular evidence suggests that *Kyllinga*, *Pycreus*, and, by extension, *Queenslandiella* should be included in *Cyperus* (Muasya et al., 2002). *Cyperus hyalinus* is known from eastern Africa, Madagascar, Mauritius, India, Sri Lanka, tropical Australia (Queensland), and Malaysia (Kükenthal, 1935–1936; Kern, 1974; Haines & Lye, 1983; Koyama, 1985) and has recently been found in southern Florida, where it was apparently introduced by air traffic (Carter & Mears, 2000). Because Haines and Lye (1983: 293) described it as “a weed of sandy soils, near sea level” in eastern Africa and it is similar in habit and habitat to certain weeds in *Kyllinga*, we suspect that *C. hyalinus* could become a pest in turf, flowerbeds, and containerized nursery plants in the southeastern U.S.A. Additional research is needed to determine its potential as a weed and to clarify its taxonomic relationships.

*Cyperus laevigatus* L. and *C. serotinus* Rottb. are frequently cited as weeds (Appendix 2). Both species have lenticular achenes with the achene face adjacent to the rachilla and, thus, are classified into subgenus *Juncellus*. *Cyperus laevigatus* is cosmopolitan in tropical and warm temperate regions (Kükenthal, 1935–1936; DeFilipps, 1980c). Aquatic biotypes have been reported by Künn (1982), and this highly variable perennial sedge generally grows in saline, alkaline, or mineral soils associated with salt marshes in coastal areas or salt lakes, hot springs, or artesian wells or along rivers inland (Kükenthal, 1935–1936; Haines & Lye, 1983; Wilson, 1993; Gordon-Gray, 1995; Tucker et al., 2002). *Cyperus laevigatus* was collected along the coast of North Carolina, U.S.A., where it was reportedly introduced with ballast, but it apparently no longer exists there (Radford et al., 1968). A number of varieties were recognized by Kükenthal (1935–1936), which contemporary authors ignore. Wilson (1993) noted the presence of three forms of *C. laevigatus* in Australia and stated the need for its taxonomic study on a worldwide basis. *Cyperus serotinus* occurs from the Mediterranean region of southern Europe through much of Eurasia (Kükenthal, 1935–1936; DeFilipps, 1980c), and it is introduced sparingly in salt marshes along the mid-Atlantic coast of North America (Tucker et al., 2002). Kühn (1982) reported aquatic biotypes in *C. serotinus*, indicating it as a weed of rice fields in Asia. If introduced more widely, *C. serotinus* could pose problems for rice agriculture in North America and elsewhere.

**Eleocharis**

Eleocharis is a genus of ca. 200 species worldwide (Smith et al., 2002), about half of which are aquatic or semi-aquatic (Holm et al., 1997). Appendix 2 lists 53 species of *Eleocharis* as weeds. Of 118 species of *Eleocharis* studied by Ueno et al. (1989), all but six were shown to have C₃ photosynthesis. Holm et al. (1997) considered *E. acicularis* (L.) Roem. & Schult., *E. dulcis* Trin. ex Hensch., and *E. palustris* (L.) Roem. & Schult. to be among the world’s worst weeds and cite *E. acicularis* among the five most troublesome weeds in Asian rice paddies. Elliott (1821: 79) described *E. quadrangulata* (Scirpus quadrangulatus Michx.) as “very injurious” in rice fields of Georgia and South Carolina, U.S.A. The tubers of *E. dulcis* are consumed as Chinese water chestnuts, and the species is widely cultivated in Asia (Kern, 1974; Mabberley, 1997). Sculthorpe (1967) cited *E. acicularis* and *E. palustris* among the most broadly distributed aquatic plants in the world, and Svenson (1957) cited the cosmopolitan weed *E. geniculata* (L.) Roem. & Schult. (as *E. caribaea* (Rottb.) S. F. Blake) as the most widespread *Eleocharis* species. As shown in Appendix 2, *E. geniculata* is frequently cited as a weed and has been reported as a pest in rice (Kern, 1974) and taro paddies (Wagner et al., 1990). *Eleocharis radicans*
(Poir.) Kunth is reportedly naturalized in taro paddies in Hawaii (Wagner et al., 1990). Walters (1980) reported the South American species *E. bonariensis* Nees as naturalized on banks of estuarine rivers in France, with no indication of it being a weed.

*Eleocharis macrostachya*, *E. mamillata* H. Lindb., and *E. palustris* belong to a taxonomically perplexing complex and are widely distributed around the world, found in hydric soils in a variety of habitats, e.g., pond margins, marshes, ditches, and wet meadows (Svensson, 1957; Smith et al., 2002). All three taxa are listed as weeds in Appendix 2. Additionally, the related taxon, *E. erythropoda* Steud., is sometimes associated with disturbance (Smith et al., 2002) and, therefore, might be considered a weed. *Eleocharis palustris* and *E. mamillata* are found in both the Eastern and Western hemispheres, whereas *E. macrostachya* and *E. erythropoda* are restricted to the New World (Smith et al., 2002). *Eleocharis macrostachya* has an essentially western distribution in the U.S.A., ranging from Alaska, south through British Columbia and California, east to Mississippi, Illinois, and Wisconsin; it is also in Mexico and South America (Svensson, 1957; Smith et al., 2002). *Eleocharis macrostachya* seems to be dispersing eastward in the U.S.A. and was only recently reported from western Mississippi where it was locally abundant in hydric soils in a roadside ditch along a major highway (Bryson et al., 1996).

Although none of the primary sources used to compile Appendix 2 lists either *Eleocharis montevidensis* Kunth or *E. montana* (Kunth) Roem. & Schult. as weeds, we have included them based upon observations made in the southeastern U.S.A. *Eleocharis montevidensis* is widely distributed in North and South America and restricted to the Western Hemisphere (Svensson, 1957; Smith et al., 2002). In the southeastern U.S.A., this rhizomatous perennial is sometimes locally abundant and weedy in hydric soils of ditches, roadways, or other disturbed sites (Carter, pers. obs.). *Eleocharis montana* is a perennial restricted to the Western Hemisphere. It is probably indigenous to South America and is known from the Gulf coastal states of the southern U.S.A., the Caribbean, and throughout much of South America (Svensson, 1957; Smith et al., 2002).

In the southeastern U.S.A., *E. montana* is a weed of hydric soils in disturbed areas and roadside ditches and seems to be most common on fine-textured soils in the rice-growing areas of southern Louisiana and eastern Texas (Carter, pers. obs.).

*Eleocharis albida* is common along the Gulf and Atlantic coasts in the southeastern U.S.A.; it also occurs in Mexico and the Caribbean (Smith et al., 2002). It is often locally abundant in hydric brackish soils of disturbed open sites and ditches adjacent to salt marshes (Carter, 2005). Extensive coastal real estate development has undoubtedly facilitated the expansion of *E. albida* in the southeastern U.S.A. Although we include it in Appendix 2 because of its propensity to form extensive stands following disturbance, we do this with some reservation, because it is indigenous and is apparently invasive only in areas where humans have severely altered the habitat.*Eleocharis parvula* is frequently associated with *E. albida* along the coast in the southeastern U.S.A. (Carter, 2005); however, it is much more widely distributed, ranging throughout much of eastern North America from eastern Canada southward into Central America; it also occurs along the West Coast of North America and in Eurasia (Smith et al., 2002). Like *E. albida*, *E. parvula* can be locally abundant in disturbed, hydric, brackish soils in coastal areas; however, *E. parvula* also occurs sporadically inland. A number of salt marsh species, including the sedges *E. parvula* and *Bolboschoenus robustus* [= *Scirpus robustus* Pursh], occur 400 km from the coast in western Virginia, U.S.A., on saline soils formed by the pumping of brine wells and are thought to have been dispersed there by birds (Sauer, 1988).

*Eleocharis baldwinii* and *E. vivipara* are listed as weeds (WSSA, 1989). Both species are profuse in their vegetative proliferation and also reproduce from achenes. *Eleocharis baldwinii* is common in parts of the southeastern U.S.A., where it may be locally abundant in dense mats on disturbed moist sandy or peaty soils or floating in ponds or ditches (Carter, pers. obs.). *Eleocharis vivipara* spreads vegetatively, forming dense clumps on moist soil or tangled mats in ponds and ditches (Carter, pers. obs.). In the U.S.A., both *E. baldwinii* and *E. vivipara* are currently of minor economic importance as weeds and are probably only opportunistically weeds following disturbance by humans. However, because of their ability to proliferate vegetatively and to reproduce sexually from achenes, we suspect they could become invasive if introduced into suitable habitats outside their natural ranges.
Eleocharis ovata (Roth) Roem. & Schult. and *E. obtusa* (Willd.) Schult. are cited as weeds (Appendix 2; WSSA, 1989; Callahan et al., 1995) in North America. *Eleocharis ovata* ranges broadly in Eurasia and throughout much of Canada and the northern U.S.A. (Svenson, 1957). *Eleocharis obtusa* is common throughout much of North America and is naturalized in Hawaii (Svenson, 1957; Smith, 2002c) and in rice fields in southern Europe (Walters, 1980). Both *E. ovata* and *E. obtusa* are closely related caespitose annuals (rarely perennials), found in seasonally wet disturbed sites, margins of ponds, and ditches (Svenson, 1957). Tufts of these plants continue to increase in diameter, producing new fertile culms throughout the growing season so long as there is sufficient moisture (Bryson, pers. obs.). *Eleocharis engelmannii* Steud. and *E. lanceolata* Fernald are related taxa, similar to and easily confused with *E. ovata* and *E. obtusa* in habitat and growth characteristics. *Eleocharis engelmannii* occurs sporadically throughout much of the range of *E. obtusa* and differs from that species primarily in its shorter tubercle. *Eleocharis lanceolata* is found in the south-central U.S.A. and was collected in 1949 in California as a weed in a rice field (Smith, 2002c). Hybrids between *E. lanceolata* and closely related *E. obtusa* are known (e.g., Carr 13969, VSC). Its narrower, more cylindrical spikelet, acute scale, and narrower tubercle distinguish *E. lanceolata* from *E. obtusa* (Svenson, 1957; Smith, 2002c). *Eleocharis flavescens* (Poir.) Urb. var. *flavescens* and *E. flavescens* var. *oli-vacea* (Torr.) Gleason, like their New World relative *E. obtusa*, have become naturalized in rice fields of southern Europe (Walters, 1980).

*Eleocharis* sect. Limnochloa (P. Beauv. ex T. Lestib.) Torr. is a group of robust (for *Eleocharis*) emergent aquatics. These perennial species show considerable variation in the shape of their stems in transverse section, from terete, to triquetrous, to quadrangular (Svenson, 1957). As shown in Appendix 2, a number of species in this group are cited as weeds, including *E. acutangula* (Roxb.) Schult., *E. cellulosa* Torr., *E. dulcis*, *E. interstincta* (Vahl) Roem. & Schult., *E. mutata* (L.) Roem. & Schult., *E. philippinensis* Svenson, and *E. quadrangulata*. *Eleocharis acutangula* and *E. mutata* are widely distributed in both hemispheres (Svenson, 1957; Koyama, 1985), whereas *E. cellulosa*, *E. interstincta*, and *E. quadrangulata* are exclusively New World species (Svenson, 1957). *Eleocharis philippinensis* and *E. dulcis* are widely-ranging in the Eastern Hemisphere, where *E. dulcis* is widely introduced and naturalized from cultivation for its tubers (Chinese water chestnuts) (Kern, 1974; Koyama, 1985). Several species are cited as pests in rice fields, and given their aquatic habitat and emergent habit, it would appear that all have the potential to be weeds of rice agriculture or invasive pests of wetlands in natural areas (Kern, 1974; Holm et al., 1977; Koyama, 1985). As discussed in the Dispersal section, there is considerable potential for achenes of these species to be disseminated long distances by waterfowl.

**Fimbristylis**

There are more than 100 species of *Fimbristylis* worldwide (Kral, 2002b), and 46 are listed as weeds in Appendix 2. *Fimbristylis dichotoma* (L.) Vahl and *F. miliacea* (L.) Vahl are co-ranked as the world’s 40th worst complex of weeds (Holm et al., 1977). *Fimbristylis dichotoma* is a rapidly growing annual or perennial that thrives in poorly aerated soils with high moisture content (Holm et al., 1977). It has been reported as a weed of paddy crops, old rice fields, ditches, lawns, open wetland pastures and meadows, roadsides, cultivated lands, and along forest margins in 21 countries throughout the tropical and semitropical regions of the world including Africa, Asia, the Pacific Islands, and North and South America (Holm et al., 1977). *Fimbristylis dichotoma* is cited as a weed in pineapple, rice, roselle, teak, taro, and other upland row crops (Holm et al., 1977). In the southeastern U.S.A., *F. dichotoma*, *F. caroliniana* (Lam.) Fernald, and *F. castanea* (Michx.) Vahl are frequently weeds following mechanical disturbance of the soil (Kral, 1971).

*Fimbristylis miliacea*, a native to tropical America, is now a troublesome weed in Africa, Asia, Australia, and North and South America in 21 countries (Holm et al., 1977). It is considered a major weed in rice in Asia, but it is also a weed of taro, bananas, corn, sorghum, and sugarcane (Holm et al., 1977). *Fimbristylis miliacea*, an annual or sometimes perennial in the tropics, is reported to produce more than 1000 seeds per plant per year and without dormancy (Holm et al., 1977). Seeds of *F. miliacea* are easily dispersed and seedlings emerge rapidly on moist soil (Holm et al., 1977). Infestations can constitute 70% of all seedling weeds in agricultural
areas (Verga & Sierra, 1970), and in Malaysia, *F. miliacea* is reported to be the first sedge emerging after rice planting and the first sedge to recover following tillage (Burkill, 1935). Emergence of *F. miliacea* seedlings seems to be environmentally dependent. In Japan, rice planted mid-season reduced the number of emerging *F. miliacea* seedlings by 80% when compared to rice planted early season, and seedling emergence was even less in late-season rice plantings (Noda & Eguchi, 1965).

*Fimbristylis annua* (All.) Roem. & Schult. and *F. autumnalis* (L.) Roem. & Schult. are also listed as weeds in North America (WSSA, 1989) but are not as troublesome as *F. miliacea* in rice production in the southeastern U.S.A. At least some of the forms of *F. annua* were introduced into the U.S.A. with rice agriculture (Kral, 1971). *Fimbristylis decipiens* Kral was described from specimens collected in the U.S.A. (Kral, 1971). Because it is morphologically similar to and often occurs with *F. annua* and *F. dichotoma*, herbarium specimens of these three species are difficult to distinguish (Kral, 1971). A number of *Fimbristylis* spp. are thought to have been introduced in the U.S.A. and elsewhere around the world with rice agriculture (Appendix 1). *Fimbristylis aestivalis* (Retz.) Vahl has been reported as a weed of rice and in taro paddies in the Eastern Hemisphere and in Hawaii (Kern, 1974; Wagner et al., 1990; Ravi & Mohanan, 2002).

**Fuirena**

The 30 species of *Fuirena* worldwide are nearly all heliophytic wetland plants of acidic soils in the tropics and subtropics (Kral, 1980, 2002a). Eight species are listed in Appendix 2, including two, *F. ciliaris* (L.) Roxb. and *F. umbellata* Rottb., cited as weeds of rice fields in the Eastern Hemisphere. *Fuirena breviseta* (Coville) Coville, *F. pumila* (Torr.) Spreng., *F. scirpoidea* Michx., *F. simplex* Vahl, and *F. squarrosa* Michx. are weeds in the U.S.A. (WSSA, 1989), where they occur in wet soils of pastures or along waterways and roadsides. None of the *Fuirena* spp. is a major weed.

**Isolepis**

*Isolepis* contains about 69 species worldwide, predominately found in cool-tropical and temperate regions of Africa and Australia (Smith, 2002d); a single species is listed as a weed in Appendix 2. *Isolepis carinata* [= *Scirpus koilolepis* (Steud.) Gleason] is occasionally a weed on moist bare soils in gardens, row crops, and natural areas, following fire or tillage (Carter et al., 1990; Bryson & Hanks, 2001). It is usually not a particularly troublesome weed in row crops because of its diminutive stature, susceptibility to foliar herbicides, and early-season phenology. *Isolepis cernua* is widely distributed around the world primarily in temperate and subtropical regions, occurring in southern Africa (absent from tropical Africa), Eurasia (absent from southeastern Asia), Australia and New Zealand, temperate South America, and North America (Wilson, 1981; Gordon-Gray, 1995; Smith, 2002d). It is apparently a recent arrival (since 1888) in the U.S.A. and Canada, where it is found primarily on the Pacific coast in fresh to brackish water on beaches, dunes, and marine bluffs (Smith, 2002d). It is also known from Texas, where the earliest collection seen by Smith (2002d) was from 1974. The taxonomy of *I. cernua* and related species is in need of revision on a worldwide basis to clarify relationships of taxa and complex nomenclature (Wilson, 1981; Gordon-Gray, 1995). According to Smith (2002d), only *I. cernua* var. *cernua* is known from North America. Although no citations were found of *I. cernua* as a weed, it is included here because of its apparent introduction into the U.S.A. and its potential to be introduced and naturalized elsewhere in temperate and subtropical areas through the ornamental trade (Bailey, 1935; Everett, 1980–1982; Grounds, 1989; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999).

**Kyllinga**

*Kyllinga*, a genus of short rhizomatous perennials or caespitose annuals, consists of 40 to 45 species distributed in tropical, subtropical, and warm temperate regions around the world (Tucker, 1984, 1987, 2002b). Appendix 2 lists 13 species as weeds, and *K. brevifolia* is among the world’s worst weeds, having been reported in 17 crops and 43 countries (Holm et al., 1997). The maximum diversity of *Kyllinga* occurs in tropical East Africa and Madagascar, where there are 30 to 35 species (Kükenthal, 1935–1936; Haines & Lye, 1983). An additional 11 to 12 *Kyllinga* species occur in Asia and two occur in Australia; none is native to Europe and only one is thought to be native to North America. *Kyllinga brevifolia*, *K. gracillima*, *K. odorata* Vahl, *K. pumila* Michx., and *K. squamula-
ta are known from the continental U.S.A. (Kartesz, 1994). *Kyllinga brevifolia* and *K. nemoralis* (J. R. Forst. & G. Forst.) Dandy ex Hutch. & Dalziel are introduced weeds in Hawaii (Delahoussaye & Thieret, 1967; Holm et al., 1979; Tucker, 1987). *Kyllinga polyphylla* Willd. ex Kunth, a native of Africa, is introduced into Samoa, Tahiti, and Fiji, where it is a weed of disturbed places, pastures, and roadsides at elevations up to 700 m (Whistler, 1994). Spreading by rhizomes, it is a particularly serious pest in pastures because it displaces acceptable forage and is not eaten by livestock (Whistler, 1994).

*Kyllinga pumila*, a weed of lawns and turf, was initially described in the first North American flora by Michaux (1803) and is evidently the only *Kyllinga* species native to the continental U.S.A. *Kyllinga brevifolia*, *K. gracillima*, *K. odorata*, and *K. squamulata* are all pantropical species (Reed, 1977; Holm et al., 1979; Tucker, 1984, 1987; Koyama, 1985) and were apparently all introduced into the continental U.S.A. from Asia. Although the precise time of their introductions is unknown, *K. brevifolia* was established in the U.S.A. prior to 1821 (Elliott, 1821), and *K. odorata* before 1836 (Torrey, 1836). Both are widespread in the eastern U.S.A., especially in the southern Atlantic and Gulf coastal plains, and are introduced weeds of South America (Bryson et al., 1996; Kissmann, 1997). In the U.S.A., distributions and recent range expansions indicate later introductions for *K. gracillima* and *K. squamulata* (Delahoussaye & Thieret, 1967; Sipple, 1978; Ferren & Schuyler, 1980; Kral, 1981; Webb & Dennis, 1981; Webb et al., 1981; Wunderlin, 1982; Snyder, 1983, 1984; Naczi, 1984; Naczi et al., 1986; Sundell & Thomas, 1988; Bryson & Carter, 1992, 1994; Mears & Libby, 1995; Bryson et al., 1996). *Kyllinga brevifolia* and *K. odorata* have continued to spread northward and westward in the U.S.A., especially as weeds of turf, pastures, and roadways (Bryson & Carter, 1992, 1994; Jones et al., 1993; Bryson et al., 1996), while *K. gracillima* continues to spread south and westward (Sipple, 1978; Ferren & Schuyler, 1980; Kral, 1981; Webb & Dennis, 1981; Webb et al., 1981; Snyder, 1983, 1984; Naczi, 1984; Naczi et al., 1986; Sundell & Thomas, 1988; Bryson & Carter, 1992, 1994; Mears & Libby, 1995; Bryson et al., 1996, 1997).

The small achenes of the introduced *Kyllinga* spp. could have arrived in the U.S.A. by a variety of dispersal methods. Following introduction, *Kyllinga* probably first naturalized along sandbars and disturbed areas along streams or in open ruderal sites with adequate moisture. *Kyllinga* spp. are common weeds of highly maintained, frequently irrigated turf in urban areas and on golf courses, and such sites now provide excellent habitat for local proliferation, dispersal, and range expansion of populations (Yelverton, 1996). *Kyllinga* spp. are also frequent weeds of mulched irrigated flowerbeds and containerized nursery plants (Whitwell & Smith, 1997).

*Kyllinga brevifolia* and *K. gracillima* are rhizomatous perennials, and *K. odorata*, *K. pumila*, and *K. squamulata* are annuals or short-lived perennials in warmer climates. *Kyllinga brevifolia* flowers 10 to 12 weeks after germination and produces mature seeds three weeks after flowering (Holm et al., 1997). *Kyllinga brevifolia* seeds are disseminated by wind and water and germinate without aging (Sumaryono & Basuki, 1986), and human activities result in the movement of whole plants, fragments, or seeds in sod, soil, or grass clippings. A combination of frequent (often daily) irrigation and mowing (3–6 times/week) without removal of clippings, especially around golf course greens, enhances vegetative growth of perennial *Kyllinga* species (Yelverton, 1996). *Kyllinga brevifolia* and *K. gracillima* produce culms that produce fruit below most turfgrass mowing heights (< 1.25 cm), resulting in a reproductive advantage over many other weeds, and they spread rapidly in turf via rhizome growth (Yelverton, 1996). Factors contributing to the increasing importance of *Kyllinga* species as weeds include irrigation of turf, type and timing of herbicide applications, use of fertilizer, and the expansion in the container nursery plants and turfgrass industry to meet the increasing demand for “instant,” well-maintained flowerbeds, lawns, and golf courses (Yelverton, 1996; Bryson et al., 1997).

*Kyllinga brevifolia* and *K. gracillima* are similar in appearance and difficult, if not impossible, to distinguish vegetatively (Yelverton, 1996). Collections of fruiting specimens of *K. gracillima* are primarily from late August until frost, suggesting that the initiation of flowering is dependent upon photoperiod. The more northern distribution of *K. gracillima* in the U.S.A. suggests that it can withstand cooler winter temperatures. *Kyllinga brevifolia*, *K. odorata*, *K. pumila*, and *K. squamulata* flower and produce fruit during the frost-free months throughout their ranges in the continental U.S.A. (Bryson et al., 1997).
**LEPIDOSPERMA**

*Lepidosperma* is a genus of ca. 60 species distributed in tropical and subtropical areas of China, Malaysia, Australia, New Caledonia, and New Zealand (Kern, 1974; Mabberley, 1997). One species, *L. chinense* Nees & Meyen, grows in rice fields in southern China (Kern, 1974) and is cited as a weed in Appendix 2.

**LEPIRONIA**

*Lepironia* Rich. is a genus of five species distributed in Polynesia and Madagascar (Mabberley, 1997). *Lepironia articulata* (Retz.) Domin, cultivated for fibers used in sails and as packing material (Mabberley, 1997), is a weed of rice fields in Malaysia (Moody, 1989) and is cited in Appendix 2.

**LIPOCARPHA**

*Lipocarpha* R. Br. (including *Hemicarpha* Nees) consists of ca. 35 species of wet pantropical and warm temperate regions (Tucker, 2002c). In Appendix 2, three species are cited as weeds of rice or other wet agricultural fields: *Lipocarpha chinensis* (Osbeck) J. Kern, *L. microcephala* (R. Br.) Kunth, and *L. squarrosa* (L.) Goetgh. (Lin, 1968; Kern, 1974; Holm et al., 1979; Kühn, 1982; Koyama, 1985). Additionally, we have observed *L. maculata* (Michx.) Torr. in the southeastern U.S.A. as a weed of disturbed hydric soils, poorly kept moist lawns, roadsides, and ditches. Based upon our observations of its habitat and the citation of congeners as weeds in the Eastern Hemisphere (Kern, 1974; Koyama, 1985), we suspect that *L. maculata* could become a weed in rice fields in the U.S.A. and elsewhere.

**MAPANIA**

*Mapania* (including *Thoracostachyum* Kurz) is a genus of 73 species distributed in tropical and subtropical areas of Asia (Mabberley, 1997). *Mapania cuspidata* (Miq.) Uitten grows in rice fields in Indonesia (Moody, 1989) and is cited as a weed in Appendix 2.

**OXYCARYUM**

*Oxycaryum* Nees is a monotypic genus widely distributed in the tropics and subtropics of Africa and the Americas (Bruhl, 2002). The only species, *O. cubense*, is in the West Indies (Kunth, 1837), South and Central America (Nees von Esenbeck, 1842; Adams, 1994), the southeastern U.S.A. (Chapman, 1889; Small, 1933; Godfrey & Wooten, 1979; Tucker, 1987), and tropical Africa (Lye, 1971; Hooper & Napper, 1972; Haines & Lye, 1983). In the southeastern U.S.A., it occurs sporadically in Florida (Chapman, 1889; Clewell, 1985; Wunderlin, 1998), southern Georgia (Bryson et al., 1996), southern Alabama (Mohr, 1901; Leong, 1988), Louisiana (Thomas & Allen, 1993), and coastal Texas (Correll & Johnston, 1970; Hatch et al., 1990; Jones et al., 1997). *Oxycaryum cubense* has spirally arranged scales and has been treated as *Scirpus cubensis* Poepp. & Kunth (e.g., Correll & Johnston, 1970; Godfrey & Wooten, 1979); however, its habit and embryo resemble *Cyperus* (van der Veken, 1965; Lye, 1971), and its taxonomic placement has been disputed: *Cypereae* (Lye, 1971) and *Scirpeae* (Bruhl, 1995). The molecular analysis of Muasya et al. (2002) supports classification of *Oxycaryum* in *Cypereae*. Two forms differing only in gross inflorescence features occur throughout the range of the species. Plants with umbellate inflorescences are called *O. cubense* f. *cubense*, while those with monoecephalous inflorescences are called *O. cubense* f. *paraguayense* (Maury) Pedersen (Barros, 1960; Pedersen, 1995). This aquatic species forms extensive floating rafts in ponds, lakes, ditches, or impounded swamps in the southeastern U.S.A. and elsewhere (Haines & Lye, 1983; Bryson et al., 1996). *Oxycaryum cubense* is one of the most vigorous plants (along with *Salvinia molesta* D. S. Mitch. and *Pistia stratiotes* L.) in forming sudds in African lakes (Holm et al., 1977), thereby impeding navigation. In the southeastern U.S.A., *O. cubense* appears to be invasive, with floating mats covering large areas to the exclusion of other aquatic vegetation (Bryson et al., 1996); however, its sporadic distribution in the U.S.A. suggests low fertility of achenes. Its corky buoyant achenes are adapted to dispersal by moving water, and its mat-forming, floating habit facilitates asexual reproduction and transport of vegetative fragments by moving water (Haines & Lye, 1983). *Oxycaryum cubense* has been in the southeastern U.S.A. for more than a century (Chapman, 1889; Mohr, 1901), and we suspect that it was dispersed into North America from the West Indies or South America by migratory birds or with ballast. In order to understand better its dispersal and potential to
invade wetland habitats, additional research into its reproductive biology is needed to determine the extent to which *O. cubense* reproduces sexually and spreads from achenes.

**RHYNCHOSPORA**

*Rhynchospora* is a cosmopolitan genus of more than 250 species, most of which inhabit wet, acidic soils (Kral, 2002e). *Rhynchospora* spp. are of little economic importance as weeds, and 20 species are listed in Appendix 2. Although most *Rhynchospora* spp. considered to be weeds are only secondarily or occasionally so, *R. corymbosa* (L.) Britton, *R. holoschoenoides* (Rich.) Herter, *R. submarinata* Kük., and *R. wightiana* (Nees) Steud. are cited as weeds of rice agriculture in the Eastern Hemisphere (Kern, 1974; Simpson & Inglis, 2001). In the U.S.A., *R. corniculata* (Lam.) A. Gray and *R. globularis* (Chapm.) Small are occasionally weeds (WSSA, 1989) along ground transportation routes but usually do not cause economic losses, and dense stands of the caespitose perennial, *R. corniculata*, along waterways impede flow in canals associated with rice production and can cause unwanted flooding of agricultural fields. Several species related to *R. corniculata* are sometimes locally abundant in roadside ditches in the Coastal Plain of the eastern U.S.A. *Rhynchospora macrostachya* Torr. ex A. Gray and *R. corniculata* are found in hydric soils in a variety of wetland habitats, including roadside ditches and margins of artificial ponds, and both are caespitose perennials of wide distribution in eastern North America (Kral, 2002e). The related species, *R. inundata* Fernald and *R. careyana* Fernald, are emergent rhizomatous perennials that form extensive stands in shallow depressions in the flatwoods, including roadside ditches (Kral, 2002e). Although only *R. corniculata* is listed as a weed, we suspect that *R. careyana*, *R. inundata*, and *R. macrostachya* might be invasive, if introduced into similar habitats outside of their natural ranges. *Rhynchospora caduca* Elliott, of little value as forage for livestock, is sometimes a weed in poorly maintained pastures in the southeastern U.S.A. where it is native (Bryson, pers. obs.) and is recently introduced and spreading rapidly in Hawaii (Wagner et al., 1990; Wagner & Herbst, 1995). *Rhynchospora globularis*, another native of the continental U.S.A., was collected in 1982 as an introduction in Hawaii (Wagner et al., 1990) and also occurs in northern California (Cranfil, 1993) where it is perhaps introduced from the eastern U.S.A. Other *Rhynchospora* spp. that opportunistically spread into artificially disturbed sites within their native ranges in the southeastern U.S.A. include *R. cephalantha* A. Gray, *R. debilis* Gale, *R. fascicularis* (Michx.) Vahl, *R. glomerata* (L.) Vahl, *R. fernaldii* Gale, *R. in expansa* (Michx.) Vahl, *R. microcephala* (Britton) Britton ex Small, *R. odorata* C. Wright ex Griseb., and *R. torreyana* A. Gray (Godfrey & Wooten, 1979; Bryson & Carter, pers. obs.). We suspect that such plants would likely become invasive if introduced into suitable habitats elsewhere, as *R. caduca* has in Hawaii.

**SCHOENOPLECTUS**

*Schoenoplectus* is a genus of 77 species worldwide (Smith, 2002b), of which 20 are cited as weeds in Appendix 2. *Schoenoplectus mucronatus* (L.) Palla [= *Scirpus mucronatus* L.], considered to be among the world’s worst weeds (Holm et al., 1997), is a pest in rice and other row and tree crops in Bangladesh, France, India, Malaysia, the Philippines, Portugal, Spain, and the U.S.A. (Holm et al., 1997). *Schoenoplectus mucronatus* is a greater problem in paddy fields where hand labor is the primary method of weed control than in rice production involving mechanical tillage and the use of herbicides. *Schoenoplectus grossus* (L. f.) Palla [= *Scirpus grossus* L. f.] is a weed of rice, riverbeds, reservoirs, and irrigation systems in southeastern Asia including regions of Vietnam, India, and the Philippines, and *S. tabernaemontani* is also listed as a weed of rice in China (Zhirong et al., 1990). *Schoenoplectus juncoides* (Roxb.) Palla is reportedly naturalized in rice fields in Europe (DeFilippis, 1980a). *Schoenoplectus acutus* and *S. americanus* (Pers.) Volkart ex Schinz & R. Keller are weeds in wetland areas of North America (WSSA, 1989; Callahan et al., 1995), while *S. californicus* (C. A. Mey.) Sojak is reported as a weed in North America and Brazil (WSSA, 1989; Kissmann, 1997).

**SCIRPODENDRON**

*Scirpodendron* Zipp. ex Kurz is a genus of two species ranging from Sri Lanka and southeastern Asia through Malesia to Australia and Polynesia (Goetghhebeur, 1998). *Scirpodendron* inhabits fresh-
water tidal swamps, tidal swamp forests, and forests adjacent to mangroves, and its large fruits are dispersed by water (Kern, 1974). It is cultivated in Sumatra for its leaves, which are used for thatching and weaving mats and hats (Kern, 1974). *Scirpodendron ghaeri* (Gaertn.) Merr. has been cited as a weed of rice fields in Asia (Moody, 1989).

**SCIRPUS**

*Scirpus* is a genus of 35 species widely distributed in North America, Mexico, Eurasia, Australia, and the Pacific Islands (Whittemore & Schuyler, 2002). Eight species are listed as weeds in Appendix 2, none of which is invasive in agricultural croplands. *Scirpus atrovirens* Willd., *S. pendulus* Muhl., and *S. cyperinus* (L.) Kunth are native to North America and cited as weeds there (WSSA, 1989; Callahan et al., 1995). These *Scirpus* species are occasional weeds along roadsides and waterways and in wet pastureland but rarely cause economic losses. *Scirpus atrovirens* and *S. pendulus* are naturalized in Europe (DeFilipps, 1980a). In the U.S.A., where it is native, *S. cyperinus* sometimes forms extensive stands dominating disturbed wetlands (Carter, pers. obs.), and we strongly suspect it would be an invasive pest if introduced into suitable habitats outside its natural range.

**SCLERIA**

*Scleria* is widely distributed in tropical and subtropical regions around the world and consists of ca. 200 species (Reznicek et al., 2002). As shown in Appendix 2, 24 species are weeds, a number of which are aquatics and known or potential weeds of rice agriculture (e.g., *Scleria biflora* Roxb., *S. laevis* Retz., *S. lithosperma* (L.) Sw., *S. novae-hollandiae* Boeckeler). The non-native invasive weed *Scleria lacustris* C. Wright has been found in freshwater marshes of peninsular Florida, U.S.A., where it can be locally abundant and dominant in water up to 1 m deep, forming dense stands and displacing native vegetation (Tobe et al., 1998; Wunderlin, 1998; Jacono, 2001). *Scleria lacustris* seems to require recession of standing water in order to become established (Jacono, 2001). It is thought to be native in scattered areas of the Neotropics, Africa, and Madagascar (Core, 1933; Hennessy, 1985) and is known from Brazil, Cuba, Costa Rica, French Guiana, Guyana, Jamaica, Paraguay, Suriname, U.S.A., and six countries across tropical Africa (Jacono, 2001). Additional research is needed to determine the ecological range of *S. lacustris* and control strategies. *Scleria vaginata* Steud. is an aggressive vine native to Central and South America that was collected once in southern Florida, U.S.A. (Reznicek et al., 2002), and we suspect it could be invasive if introduced into tropical and subtropical areas outside its native range.

**DISCUSSION**

Cyperaceae is a large, diverse, cosmopolitan family, and many of its species are biologically predisposed to spread opportunistically into areas altered by humans. Data compiled in Appendix 1 show that humans have played a tremendous role in the dispersal of sedges, including many weeds. Given the fundamental importance of dispersal and habitat disturbance in the evolution and survival of weeds and their intrinsic attributes favoring competition, colonization, and migration, it is not surprising that many sedges have evolved and continue to evolve as weeds. The magnitude of the human “footprint” on Earth is immense. Given the role that humans play in destruction and conversion of natural areas into disturbed and highly artificial ruderal habitats and urban and agricultural systems, it is axiomatic that the numbers of noxious weeds and invasive plant species will increase in step with the human population.

It is difficult to anticipate which species will become weeds, and where and under what circumstances they will be invasive. *Rhynchospora caduca*, a seemingly innocuous sedge native to the southeastern U.S.A., has recently been reported as an invasive weed in Hawaii (Wagner & Herbst, 1995). *Rhynchospora caduca* is not extraordinary among the beak-rushes in the southeastern U.S.A., which suggests that any number of apparently harmless species could pose similar problems in an alien environment. Insular systems, such as the Hawaiian Islands, have great potential as natural laboratories for the study of invasion.

Appendix 2 is a list of 447 species of Cyperaceae cited as weeds, which was compiled from more than 60 publications. Most cyperaceous weeds are from tropical and subtropical regions, and the most trou-
blesome sedges (*Cyperus rotundus*, *C. esculentus*, *C. difformis*, and *C. iria*) are native to Asia and Africa but are now widely dispersed on other continents.

In order to examine the impact of humans on dispersal and introduction of cyperaceous weeds, we noted commonalities in listings of species in Appendices 1 and 2 and used these data to construct Table 4. Thus, Table 4 shows the number of weed species in each genus that are known or suspected to have been anthropogenically dispersed. When Appendices 1 and 2 are compared, 111 species are common to both lists (Table 4) with the greatest number of cyperaceous weeds known or suspected to be dispersed by humans in *Cyperus* (43 spp., ca. 39%), followed by *Carex* (24 spp., ca. 22%); *Eleocharis* (9 spp., ca. 8%); *Fimbristylis* (8 spp., 7%); *Kyllinga* and *Schoenoplectus* (6 spp. each, 5%); *Scirpus* (5 spp. each, ca. 5%); *Rhynchospora* (3 spp., ca. 3%); *Fuirena* (2 spp., ca. 2%); and *Bolboschoenus*, *Bolbosstylis*, *Lepironia*, *Lipocarpha*, and *Mapania* (1 spp. each, ca. 1%).

*Carex*, by far, has been subject to greater anthropogenic dispersal than the other cyperaceous genera, which undoubtedly has been an important factor. It is readily concluded from Appendix 1 that *Cyperus* spp. have been mostly introduced unintentionally through a variety of human activities, especially as contaminants of seeds (particularly rice), wool, and dumping of ship’s ballast. It seems reasonable to conclude from these data that systematic surveys of flora in vicinity of ports of entry are needed for early detection of new introductions and reintroductions and to understand better the dynamics of inadvertent importation of noxious weeds.

The role of rice agriculture in the introduction of cyperaceous weeds has long been recognized and is reinforced by data presented in Appendix 1. The number of cyperaceous weeds associated with rice agriculture in Appendix 2 is great, and, despite advancements in the regulation of importation of grain, there still exists the possibility of unintentional movement and introduction of other potentially noxious sedges as contaminants in shipments of seeds. These data indicate the need for continued vigilance and regulation of movement and importation of sedges throughout the world.

Historically, *Carex* spp. have received little attention as agricultural weeds. However, Kukkonen (2001) includes rice fields in Pakistan as habitats of *Carex diandra*, *C. pycnostachya*, and *C. divisa* Huds., and he describes *C. songorica* Kar. & Kir., *C. dilata* M. Bieb., and *C. orbicularis* Boott as growing in irrigation channels. The latter set of species is not listed in Appendix 2, which includes only entries explicitly characterized as weeds or invasives or directly associated with agricultural fields, gardens, or turf. However, populations of native sedges that have spread into irrigation canals associated with agriculture have certainly adapted to human disturbance, and biotypes adapted to conditions in the adjacent fields could easily evolve.

The large number of ornamental and cultivated sedges (>150 spp.) listed in Appendix 1 was not anticipated. Of particular interest is the increasing horticultural usage of sedges, especially *Carex* spp., as ornamentals (Figs. 2 and 3). This indicates a need for increased research into the reproductive biology, physiology, and growth characteristics of ornamental sedges to determine which species may be safely used and where and which will likely become invasive. There is also a need for greater awareness about problems inherent in the unwise and irresponsible use of ornamental sedges and additional measures toward intervention to prevent the transportation and importation of ornamental sedges.

Because of their distributions across vast latitudinal, altitudinal, and climatic ranges and diverse habitats, populations of widely distributed weeds have been subject to a great array of environmental factors resulting in much localized natural (and artificial) selection and diversification. Thus, in general, the taxonomy of weeds is far more complex than of other plants, which is evident in the complex nomenclature of the most widely distributed weeds, e.g., *Cyperus esculentus*, *C. rotundus* (Haines & Lye, 1983), *C. polystachyos* (cf. Kükenthal, 1935–1936), and *C. sanguinolentus* (cf. Kükenthal, 1935–1936; Kern, 1974). To resolve basic questions about relationships within these taxa, there is a great need for additional morphometric, field-, and herbarium-based research into the variation and taxonomy on a worldwide basis. The increased use of molecular techniques (e.g., Muasya et al., 2000a, b, 2002) should help to stabilize nomenclature by resolving the taxonomic status and rank of certain disputed groups, e.g., the segregates of *Cyperus* and *Scirpus*. In the future, the results of molecular research will elucidate much about the pathways of introduction.
and migration of invasive weeds. Introduction of new weeds is increasingly a problem because of the frequency and ease of long-distance and international transportation, and advances in basic research will result in molecular assays useful in detecting and stopping weeds at ports of entry and in more accurately diagnosing infestations of herbicide-resistant biotypes of weeds.

Given the economics of weed control, including indirect costs (e.g., increased cost of health care, remediation of environmental damage), every precaution should be taken to avoid tagging indigenous plants as weeds without compelling supportive evidence. Realistically and pragmatically, it is most certainly advantageous and desirable for native plants to occupy roadsides and other artificial habitats than alien weeds. There is a great need for basic research to determine the ecological tolerances and invasive potentials and limits of indigenous and nonindigenous weeds. For only through the results of such research will basic knowledge be advanced sufficiently to allow applied scientists, natural resource managers, and the public to make informed, intelligent decisions about which plants to promote, which to exclude, which to suppress, and when to suppress them.

**Table 4.** Numbers and percentages of species of Cyperaceae by genus, which have been cited as weeds and are known or suspected to be dispersed by humans (data extracted from Appendices 1 and 2).

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species (incl. infrasp.)</th>
<th>Percent of Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyperus^2</td>
<td>43</td>
<td>39</td>
</tr>
<tr>
<td>Carex</td>
<td>24</td>
<td>22</td>
</tr>
<tr>
<td>Eleocharis</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>Fimbristylis</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>Kylinga</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Schoenoplectus</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Scirpus</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Rhynchospora</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Fuirena</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Bolboschoenus</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Bulbosylis</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Lepironia</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Lipocarpha</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mapania</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Abildgaardia</td>
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<td>0</td>
</tr>
<tr>
<td>Caustis</td>
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<td>0</td>
</tr>
<tr>
<td>Cladium</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Courtoisina</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cymophyllus</td>
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<td>0</td>
</tr>
<tr>
<td>Desmoschoenus</td>
<td>0</td>
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</tr>
<tr>
<td>Eriophorum</td>
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<td>0</td>
</tr>
<tr>
<td>Cahnia</td>
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<td>0</td>
</tr>
<tr>
<td>Isolepis</td>
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</tr>
<tr>
<td>Kobresia</td>
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<td>0</td>
</tr>
<tr>
<td>Lepidosperma</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Machaerina</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Oreobolus</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Oxycaryum</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Schoenus</td>
<td>0</td>
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</tr>
<tr>
<td>Scleria</td>
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<td>0</td>
</tr>
<tr>
<td>Trichophorum</td>
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<td>0</td>
</tr>
<tr>
<td>Uncinia</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>111</strong></td>
<td>~100</td>
</tr>
</tbody>
</table>

1 Authority names for genera in Table 4 not discussed elsewhere in this paper are as follows: Caustis R. Br.; Desmoschoenus Hook f.; Kobresia Willd.; Oreobolus R. Br.; Schoenus L.; Trichophorum Pers.

2 Includes Diclidium, Juncellus, Mariscus, Pycreus, and Queenslandiella.

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The Significance of Cyperaceae as Weeds


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## Appendix 1

Known and suspected anthropogenic dispersal in Cyperaceae.

<table>
<thead>
<tr>
<th>Species</th>
<th>Method of dispersal</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bolboschoenus glaucus</em> (Lam.) S. G. Sm.</td>
<td>planted as waterfowl food, rice agriculture</td>
<td>Browning et al., 1995; Smith, 2002a</td>
</tr>
<tr>
<td><em>Bolboschoenus maritimus</em> (L.) Palla</td>
<td>rice agriculture</td>
<td>Holm et al., 1997</td>
</tr>
<tr>
<td><em>Bolboschoenus maritimus</em> subsp. <em>paludosus</em> (A. Nelson) T. Koyama</td>
<td>planted as waterfowl food</td>
<td>Smith, 2002a</td>
</tr>
<tr>
<td><em>Bolboschoenus robustus</em> (Pursh) Sojak</td>
<td>ornamental</td>
<td>Everett, 1980–1982</td>
</tr>
<tr>
<td><em>Bulboschius humilis</em> (Kunth) C. B. Clarke</td>
<td>wool alien</td>
<td>Sell &amp; Murrell, 1996</td>
</tr>
<tr>
<td><em>Bulboschius striatella</em> C. B. Clarke</td>
<td>wool alien</td>
<td>Sell &amp; Murrell, 1996</td>
</tr>
<tr>
<td><em>Carex acuta</em> L.</td>
<td>ornamental</td>
<td>Grounds, 1989; Huxley, 1992</td>
</tr>
<tr>
<td><em>Carex acutiformis</em> Ehrh.</td>
<td>ornamental</td>
<td>Huxley, 1992</td>
</tr>
<tr>
<td><em>Carex alba</em> Scop.</td>
<td>ornamental</td>
<td>Huxley, 1992</td>
</tr>
<tr>
<td><em>Carex albula</em> Allan</td>
<td>ornamental</td>
<td>Greenlee &amp; Fell, 1992; Turner &amp; Wasson, 1998; Darke, 1999</td>
</tr>
<tr>
<td><em>Carex appressa</em> R. Br.</td>
<td>erosion control, wool alien</td>
<td>Huxley, 1992; Sell &amp; Murrell, 1996; Simpson &amp; Inglis, 2001</td>
</tr>
<tr>
<td><em>Carex arenaria</em> L.</td>
<td>ornamental</td>
<td>Huxley, 1992</td>
</tr>
<tr>
<td><em>Carex atrata</em> L.</td>
<td>ornamental</td>
<td>Grounds, 1989; Huxley, 1992</td>
</tr>
<tr>
<td><em>Carex austriaca</em> Mack.</td>
<td>railroad adventive</td>
<td>Mühlenbach, 1983</td>
</tr>
<tr>
<td><em>Carex baccans</em> Nees</td>
<td>ornamental</td>
<td>Bailey, 1935; Greenlee &amp; Fell, 1992; Huxley, 1992; Darke, 1999</td>
</tr>
<tr>
<td><em>Carex baldensis</em> L.</td>
<td>ornamental</td>
<td>Huxley, 1992</td>
</tr>
<tr>
<td><em>Carex baltzelli</em> Chapm. ex Dewey</td>
<td>ornamental</td>
<td>Darke, 1999</td>
</tr>
<tr>
<td><em>Carex berggreni</em> Petrie</td>
<td>ornamental</td>
<td>Grounds, 1989; Huxley, 1992; Darke, 1999</td>
</tr>
<tr>
<td><em>Carex brevior</em> (Dewey) Mack. ex Lunell</td>
<td>contaminated grass seed</td>
<td>Bryson et al., 1992</td>
</tr>
<tr>
<td><em>Carex brunnea</em> Thunb.</td>
<td>ornamental</td>
<td>Grounds, 1989; Huxley, 1992</td>
</tr>
<tr>
<td><em>Carex buchananii</em> Berggr.</td>
<td>ornamental</td>
<td>Bailey, 1935; Brooklyn Botanical Garden, 1988; Ottesen, 1989; Greenlee &amp; Fell, 1992; Darke, 1999</td>
</tr>
<tr>
<td><em>Carex caryophyllea</em> Latourr.</td>
<td>ornamental</td>
<td>Huxley, 1992; Darke, 1999</td>
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### Appendix 1. Continued.

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<tr>
<td><em>Cyperus surinamensis</em> Rottb.</td>
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<td>Britton, 1886</td>
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<tr>
<td><em>Cyperus tenuis</em> Sw.</td>
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<tr>
<td><em>Cyperus textilis</em> Thunb.</td>
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<tr>
<td><em>Cyperus umbellatus</em> Benth.</td>
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<td>Brown, 1880</td>
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<td><em>Cyperus vaginatus</em> R. Br.</td>
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### Appendix 1. Continued.

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<td><em>Eleocharis interstincta</em> (Vahl) Roem. &amp; Schult.</td>
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<td><em>Eleocharis lanceolata</em> Fernald</td>
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<td><em>Eleocharis macrostachya</em> Britton</td>
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<td><em>Eleocharis pachycarpa</em> E. Desv. in C. Gay</td>
<td>sheep industry</td>
<td>Svenson, 1957</td>
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<td><em>Eleocharis palustris</em> (L.) Roem. &amp; Schult.</td>
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<td><em>Eriophorum latifolium</em> Hoppe</td>
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<td><em>Eriophorum scheuchzeri</em> Hoppe</td>
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<td>Fosberg, 1988</td>
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<td>Burkill, 1935</td>
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<td><em>Fimbristylis spadicea</em> Vahl</td>
<td>ballast</td>
<td>Smith, 1867</td>
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<tr>
<td><em>Fimbristylis squarrosa</em> Vahl</td>
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<td>Species</td>
<td>Method of dispersal</td>
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<td><em>Fuirena squarrosa</em> Michx.</td>
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<td><em>Isolepis prolifera</em> (Rottb.) R. Br.</td>
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<td><em>Isolepis setacea</em> (L.) R. Br.</td>
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<td>Huxley, 1992</td>
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<td><em>Kobresia pygmaea</em> C. B. Clarke in Hook. f.</td>
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<td><em>Kyllinga brevifolia</em> Rottb.</td>
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<td>Koyama, 1985; Bryson &amp; Carter, 1992; Sell &amp; Murrell, 1996; Holm et al., 1997; Bryson et al., 1997</td>
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<td><em>Kyllinga erecta</em> Schumach.</td>
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<td><em>Kyllinga gracillima</em> Miq.</td>
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<td><em>Kyllinga nemoralis</em> (J. R. Forst. &amp; G. Forst.) Dandy ex Hutch. &amp; Dalziel</td>
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<td><em>Kyllinga odorata</em> Vahl</td>
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<td><em>Lepironia articulata</em> (Retz.) Domin</td>
<td>fibers in sails and as packing material</td>
<td>Mabberley, 1997</td>
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<td><em>Lipocarpha maculata</em> (Michx.) Torr.</td>
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<td><em>Lipocarpha micrantha</em> (Vahl) G. C. Tucker</td>
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<td><em>Machaerina sinclairii</em> (Hook. f.) Koyama</td>
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<td><em>Mapania cuspidata</em> (Miq.) Uittien</td>
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<td>Bailey, 1935; Simpson, 1992; Simpson &amp; Inglis, 2001</td>
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<td>Bailey, 1935</td>
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<td><em>Rhynchospora colorata</em> (L.) H. Pfeiff.</td>
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<td>Simpson &amp; Inglis, 2001</td>
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<td><em>Rhynchospora corymbosa</em> (L.) Britton</td>
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### Species

<table>
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<tr>
<th>Species</th>
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<th>Source</th>
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<td>Rhynchospora fuscus (L.) W. T. Aiton</td>
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<td>Huxley, 1992; Simpson 1993; Simpson &amp; Inglis, 2001</td>
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<td>Smith et al., 1993</td>
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<td>Schoenoplectus grossus (L. f.) Palla</td>
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<td>Holm et al., 1997</td>
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<td>Schoenoplectus heterochaetus (Chase) Sojak</td>
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<td>Everett, 1980–1982</td>
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<td>Bailey, 1935; Everett, 1980–1982</td>
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<td>Schoenoplectus mucronatus (L.) Palla</td>
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<td>Bailey, 1935; Darke, 1999</td>
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<td>Scirpus divaricatus Elliott</td>
<td>railroad adventive</td>
<td>Mühlenbach, 1979</td>
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<td>Scirpus georgianus R. M. Harper</td>
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<td>Mühlenbach, 1983</td>
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<td>Whittemore &amp; Schuyler, 2002</td>
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<td>Scirpus pendulus Muhl.</td>
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<td>Whittemore &amp; Schuyler, 2002</td>
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<td>Trichophorum alpinum (L.) Pers.</td>
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<tr>
<td>Uncinia egmontiana Hamlin</td>
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1 Plant nomenclature follows *Flora of North America*, volume 23; plant names were also verified through the Missouri Botanical Garden's TROPICOS VAST database (rev. 1.5) (http://mobot.mobot.org/W3T/Search/vast.html) and the International Plant Names Index (http://www.ipni.org/index.html). A more inclusive list of names cited in the references is available from the authors.
## Appendix 2

Cyperaceous weeds of the world with data on habit, habitat, and distribution.

<table>
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<th>Species</th>
<th>Source</th>
<th>Habit&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Habitat</th>
<th>Distribution&lt;sup&gt;3&lt;/sup&gt;</th>
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<td><em>Abildgaardia ovata</em> (Burm. f.) Kral</td>
<td>Holm et al., 1979; Soerjani et al., 1987; Moody, 1989; Kukkonen, 2001</td>
<td>P</td>
<td>pastures, rice fields</td>
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<td>P</td>
<td>rice fields</td>
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<td>P</td>
<td>aquatic, irrigation ditches</td>
<td>AUS, PI</td>
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<td><em>Bolboschoenus fluviatilis</em> (Torr.) Soják</td>
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<td>aquatic</td>
<td>ASI, AUS, NA</td>
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<td>Kern, 1974; Reed, 1977; Kühn, 1982; Moody, 1989; Holm et al., 1997; Johnson, 1997; Kissman, 1997</td>
<td>P</td>
<td>aquatic, crops, rice fields</td>
<td>AFR, ASI, CAR, EUR, IND, NA, PI, SA</td>
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<td><em>Bolboschoenus planiculmis</em> (F. Schmidt) T. V. Egorova</td>
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<td>P</td>
<td>wetlands, rice fields</td>
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<td>Godfrey &amp; Wooten, 1979; Lorenzi, 1982; Moody, 1989; Kiskima, 1997</td>
<td>A</td>
<td>roadsides, waste places</td>
<td>NA, SA</td>
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<td>fallow fields, roadsides, waste places</td>
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<td><em>Bulbostylis densa</em> (Wall.) Hand.-Mazz.</td>
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<td>aquatic biotypes, crops, cultivated fields, rice fields, waste places</td>
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<td>AFR</td>
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<td>Kühn, 1982; Le Bourgeois &amp; Merlier, 1995; Simpson &amp; Inglis, 2001</td>
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<td>aquatic biotypes, crops, cultivated fields, grasslands</td>
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<td>A</td>
<td>pioneers or exposed areas, weeds of cultivation</td>
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<td><em>Carex alba</em> lina Allan</td>
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<td>P</td>
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### Appendix 2. Continued.

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<th>Habitat</th>
<th>Distribution</th>
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<td>P</td>
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<td>Carex atherodes Spreng.</td>
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<td>P</td>
<td>wetlands</td>
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<td>Carex aureolensis Steud.</td>
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<td>crop borders, lawns, pastures, waste places</td>
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<td>Carex baccans Nees</td>
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<td>P</td>
<td>PI</td>
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<td>Carex blanda Dewey</td>
<td>Bryson, 1985a; DeFelice &amp; Bryson, 2004</td>
<td>P</td>
<td>lawns, waste places</td>
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<td>Carex bonariensis Desf.</td>
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<td>P</td>
<td>SA</td>
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<td>Carex brongniartii Kunth</td>
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<td>P</td>
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<td>Carex buchananii Berggr.</td>
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### Appendix 2. Continued.

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### Appendix 2. Continued.

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<td>Distribution</td>
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<td>P</td>
<td>gardens, low elevations, rice fields, warm regions</td>
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<td>Cyperus dilatatus Schumach</td>
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<td>P</td>
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<td>Cyperus distinctus Steud.</td>
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<td>Cyperus duclouxii E. G. Camus</td>
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<td>Cyperus enterrianus Boeckeler</td>
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<td>crops, pastures, roadsides</td>
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<th>Species</th>
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<td><em>Cyperus flavescens</em> L.</td>
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<td>Species</td>
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<td>Cyperus glaber L.</td>
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<td>Cyperus javanicus Houtt.</td>
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<td>Cyperus laetus J. Presl &amp; C. Presl</td>
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### Appendix 2. Continued.

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<th>Habitat</th>
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<td>Cyperus mapanioides C. B. Clarke</td>
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<td><em>Cyperus rigidifolius</em> Steud.</td>
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<td>P</td>
<td>rice fields, roadsides</td>
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**Appendix 2. Continued.**

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<td><em>Eleocharis atropurpurea</em> (Retz.) Kunth</td>
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<td><em>Eleocharis congeta</em> D. Don</td>
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<td>rice fields</td>
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<td>Cardenas et al., 1972; Kern, 1974; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Wagner et al., 1990; Kissman, 1997; Waterhouse, 1997; Kukkonen, 2001; Simpson &amp; Inglis, 2001; Ravi &amp; Mohanan, 2002</td>
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<td><em>Eleocharis kuroguwai</em> Ohwi</td>
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<td>ASI, IND</td>
</tr>
<tr>
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<td>Holm et al., 1979; Lorenzi, 1982; Kühn, 1982; WSSA, 1989; Kissman, 1997; Simpson &amp; Inglis, 2001</td>
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<td><em>Fuirena umbellata</em> Rottb.</td>
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### Appendix 2. Continued.

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<td>crops, gardens, grasslands, lawns, pastures, plantations, rice fields, roadsides, turf, waste places</td>
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<td>damp sandy ground, disturbed grassland, gardens, pastures, lawns, rice fields, turf, waste places</td>
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<td><strong>Kyllinga polyphylla</strong> Willd. ex Kunth</td>
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<td>AFR, ASI, PI</td>
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<td>crops, pastures, turf, rice fields, waste places</td>
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<td><em>Schoenoplectus juncoides</em></td>
<td>Lin, 1968; Kern, 1974; Holm et al., 1979; DeFilipps, 1980a; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; Zhirong et al., 1990; Simpson &amp; Koyama, 1998; Kukkonen, 2001; Simpson &amp; Inglis, 2001</td>
<td>A</td>
<td>aquatic biotypes, crops, rice fields</td>
<td>AFR, ASI, EUR, IND, PI</td>
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<td><em>Schoenoplectus lacustris</em></td>
<td>Holm et al., 1979; Moody, 1989; Simpson &amp; Inglis, 2001</td>
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<td>aquatic biotypes</td>
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<td><em>Schoenoplectus lacustris</em></td>
<td>Kukkonen, 2001</td>
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<td>rice fields</td>
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<td><em>Schoenoplectus lateriflorus</em></td>
<td>Kern, 1974; Soerjani et al., 1987; Moody, 1989; Kukkonen, 2001</td>
<td>A</td>
<td>rice fields</td>
<td>ASI, AUS, IND</td>
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<td><em>Schoenoplectus litoralis</em></td>
<td>Holm et al., 1979; Kühn, 1982; Simpson &amp; Inglis, 2001</td>
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<td><em>Schoenoplectus mucronatus</em></td>
<td>Kern, 1974; Reed, 1977; Holm et al., 1979, 1997; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Simpson &amp; Koyama, 1998; Kukkonen, 2001; Simpson &amp; Inglis, 2001; DeFelice &amp; Bryson, 2004</td>
<td>P</td>
<td>aquatic biotypes, ditches, rice fields, wet places</td>
<td>AFR, ASI, EUR, IND, NA, PI</td>
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<td><em>Schoenoplectus pungens</em></td>
<td>Moore &amp; Edgar, 1970; Simpson &amp; Inglis, 2001</td>
<td>P</td>
<td>aquatic, unspecified</td>
<td>AUS, CAR, EUR, NA, PI, SA</td>
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<td><em>Schoenoplectus roylei</em></td>
<td>Moody, 1989; Kukkonen, 2001; Simpson &amp; Inglis, 2001</td>
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<td>ditches, rice fields</td>
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<td><em>Schoenoplectus senegalensis</em></td>
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<td><em>Schoenoplectus tabernaemontani</em></td>
<td>Reed, 1977; WSSA, 1989; Zhirong et al., 1990</td>
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<td>aquatic, brackish water</td>
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<td><em>Schoenoplectus triqueter</em></td>
<td>Reed, 1977; Holm et al., 1979; Kühn, 1982; Moody, 1989; Zhirong et al., 1990; Kukkonen, 2001; Simpson &amp; Inglis, 2001</td>
<td>P</td>
<td>aquatic biotypes, rice fields</td>
<td>AFR, ASI, EUR, IND, PI</td>
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<td><em>Schoenoplectus wallichii</em></td>
<td>Lin, 1968; Kern, 1974; Reed, 1977; Holm et al., 1979, 1997; Moody, 1989</td>
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<td>rice fields, wet places</td>
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<td><em>Scirpodendron ghaeri</em></td>
<td>Moody, 1989</td>
<td>P</td>
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<td><em>Scirpus atrovirens</em></td>
<td>Holm et al., 1979; WSSA, 1989</td>
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<td><em>Scirpus cyperinus</em></td>
<td>Holm et al., 1979; WSSA, 1989; Carter, 2005</td>
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<td>road sides, wet places</td>
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### Appendix 2. Continued.

<table>
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<th>Species</th>
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<th>Habitat</th>
<th>Distribution</th>
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<tr>
<td><em>Scirpus giganteus</em> Kunth</td>
<td>Kissman, 1997</td>
<td>P</td>
<td>crops, waste places</td>
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<td><em>Scirpus holoschoenus</em> L.</td>
<td>Reed, 1977; Holm et al., 1979; Kühn, 1982</td>
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<td>farmland, field borders, rice fields</td>
<td>ASI, IND</td>
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<td><em>Scirpus michelianus</em> L.</td>
<td>Moody, 1989; Zhirong et al., 1990</td>
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<td>rice fields, field borders, field borders, rice fields</td>
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<td><em>Scirpus pendulus</em> Muhl.</td>
<td>Holm et al., 1979</td>
<td>P</td>
<td>rice fields, rice fields, fields</td>
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<td><em>Scirpus sylvaticus</em> L.</td>
<td>Holm et al., 1979</td>
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<td>EUR</td>
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<td><em>Scirpus triangulatus</em> Roxb.</td>
<td>Holm et al., 1979</td>
<td>P</td>
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<td><em>Scleria bancana</em> Miq.</td>
<td>Holm et al., 1979; Moody, 1989</td>
<td>P</td>
<td>rice fields</td>
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</tr>
<tr>
<td><em>Scleria boivinii</em> Steud.</td>
<td>Holm et al., 1979</td>
<td>P</td>
<td>AFR</td>
<td></td>
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<td><em>Scleria bracteata</em> Cav.</td>
<td>Holm et al., 1979; Kissman, 1997</td>
<td>P</td>
<td>NA, SA</td>
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<td><em>Scleria canescens</em> Boeckeler</td>
<td>Holm et al., 1979</td>
<td>P</td>
<td>NA, SA</td>
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<tr>
<td><em>Scleria depressa</em> (C. B. Clarke) Nelmes</td>
<td>Johnson, 1997</td>
<td>P</td>
<td>AFR</td>
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<td><em>Scleria lacustris</em> C. Wright</td>
<td>Tobe et al., 1998; Wunderlin, 1998; Jaco, 2001</td>
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<td>aquatic waste places, rice fields</td>
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<td><em>Scleria laevis</em> Retz.</td>
<td>Kern, 1974; Holm et al., 1979; Moody, 1989; Ravi &amp; Mohanan, 2002</td>
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<td>fallow rice fields</td>
<td>ASI, AUS, IND, PI</td>
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<td><em>Scleria lithosperma</em> (L.) Sw.</td>
<td>Holm et al., 1979; Kühn, 1982; Moody, 1989; Simpson &amp; Inglis, 2001</td>
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<td>aquatic biotypes, crops, rice fields, rice fields</td>
<td>AFR, ASI, IND, PI, SA</td>
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<td><em>Scleria melaleuca</em> Rchb. ex Schltdl. &amp; Cham.</td>
<td>Cardenas et al., 1972; Holm et al., 1979; Lorenzi, 1982; Moody, 1989</td>
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<td>CAR, SA</td>
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<td><em>Scleria myriocarpa</em> Steud.</td>
<td>Holm et al., 1979</td>
<td>P</td>
<td>SA</td>
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<td><em>Scleria naumanniana</em> Boeckeler</td>
<td>Akobundu &amp; Agyakwa, 1987</td>
<td>P</td>
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<td><em>Scleria novae-hollandiae</em> Boeckeler</td>
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<td>P</td>
<td>AUS, IND, PI</td>
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<td><em>Scleria oblata</em> S. T. Blake</td>
<td>Holm et al., 1979; Moody, 1989</td>
<td>P</td>
<td>rice fields</td>
<td>ASI</td>
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<td><em>Scleria poaeformis</em> Retz.</td>
<td>Holm et al., 1979; Moody, 1989</td>
<td>P</td>
<td>AFR, ASI, IND</td>
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<td><em>Scleria polycarpa</em> Boeckeler</td>
<td>Holm et al., 1979</td>
<td>P</td>
<td>PI</td>
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<td><em>Scleria purpurascens</em> Steud.</td>
<td>Holm et al., 1979; Moody, 1989</td>
<td>P</td>
<td>AFR, ASI, IND</td>
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### Species

<table>
<thead>
<tr>
<th>Species</th>
<th>Source</th>
<th>Habit</th>
<th>Habitat</th>
<th>Distribution</th>
</tr>
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<tr>
<td><em>Scleria rugosa</em> R. Br.</td>
<td>Kern, 1974; Koyama, 1985; Moody, 1989</td>
<td>A</td>
<td>rice fields</td>
<td>ASI, AUS, IND, PI</td>
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<td><em>Scleria scindens</em> Nees</td>
<td>Reed, 1977</td>
<td>P</td>
<td></td>
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<td><em>Scleria scrobiculata</em> Nees &amp; Meyen</td>
<td>Holm et al., 1979; Moody, 1989</td>
<td>P</td>
<td>rice fields</td>
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<td><em>Scleria sumatrensis</em> Retz.</td>
<td>Holm et al., 1979; Kühn, 1982; Moody, 1989; Simpson &amp; Inglis, 2001</td>
<td>A</td>
<td>aquatic biotypes, crops, forests, rice fields</td>
<td>ASI, AUS, IND, PI</td>
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<td><em>Scleria verrucosa</em> Willd.</td>
<td>Akobundu &amp; Agyakwa, 1987</td>
<td>P</td>
<td>wet areas</td>
<td>AFR</td>
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</tbody>
</table>

1. Plant nomenclature follows *Flora of North America*, volume 23; plant names were also verified through the Missouri Botanical Garden wTROPICOS VAST database (rev. 1.5) (http://mobot.mobot.org/W3T/SearchVast.html) and the International Plant Names Index (http://www.ipni.org/index.html). A more inclusive list of names cited in the references is available from the authors.


3. AFR = Africa including Madagascar; ASI = Asia; AUS = Australia; CAR = Caribbean Islands; EUR = Europe; IND = Indian subcontinent including Sri Lanka; NA = North America; PI = Pacific Islands; SA = South America.